# Molecular phylogenetics, taxonomy and niche-based conservation risk assessment of *Thesium* L. (Santalaceae)

**Daniel Andrawus Zhigila**

Thesis presented for the degree of

DOCTOR OF PHILOSOPHY

Department of Biological Sciences

UNIVERSITY OF CAPE TOWN

November 2019

Under the supervision of:

**Prof A. Muthama Muasya and A/Prof G. Anthony Verboom**

## Declaration

I, Daniel Andrawus Zhigila, know the meaning of plagiarism and hereby declare that all the work in this thesis titled "*Molecular phylogenetics, taxonomy and niche-based conservation risk assessment of Thesium L. (Santalaceae)*" except for those properly acknowledged are authentic research work carried out by me.

I hereby,

a) give the University of Cape Town free licence to reproduce the thesis in whole or some elements thereof for the purpose of research;
b) declare that this thesis in whole or in part has not been, or is being, or is to be submitted for the award of any degree or academic recognition at any University.

I have followed all the guidelines for preparing a thesis and now presenting it for examination for the award of Doctor of Philosophy.

In this thesis, I included three published papers. These papers were published in collaboration with my supervisors and research team:

Zhigila, D.A., Verboom, G.A., Stirton, C.H. and Muasya, A.M. 2019a. A taxonomic revision of *Thesium* section *Hagnothesium* (Santalaceae) and description of a new species, *T. quartzicolum. South African Journal of Botany* 124:280–303.

Zhigila, D.A., Verboom, G.A., Stirton, C.H., Smith, H. and Muasya, A.M. 2019b. Six new *Thesium* (Santalaceae) species endemic to the Greater Cape Floristic Region, South Africa, and one new name. *Phytotaxa* 423 (4):215–237.

Zhigila, D.A., Verboom, G.A. and Muasya, A.M. (accepted). An infrageneric classification of *Thesium* (Santalaceae) based on molecular phylogenetic data. *TAXON* 00 (00):1–24.

My supervisors have attested that I was principal in conceptualisation, design and data analyses of the research toward publishing the articles and that I independently wrote the manuscripts with their support in form of comments and suggestions (see Appendix 6).

**Daniel A. Zhigila** Signed by candidate **November 2019**

## Dedication

I dedicate this thesis to God the Father, God the Son and God the Holy Spirit.

**Acknowledgements**

Foremost, I wish to express my profound gratitude to my main supervisor, Prof. A. Muthama Muasya for accepting to train me, his patience, encouragement, financial support, and versatile knowledge. His mentorship and motivation helped me, not only in the context of research and thesis writing, but also the aspect of human relations.

The substance of a genius, my co-Supervisor, A/Prof. G. Anthony Verboom, I sincerely thank you for the research mentorship and insightful comments. It was such a steep learning curve, but he patiently worked with me.

I appreciate the financial fellowship by the Science Faculty, University of Cape Town (UCT). The field and laboratory works were supported by the South African National Research Foundation (Quartz fields of Southern Africa) and the Kew Herbarium visit was supported by the UCT Scholarship for International travel (Sir Robert Kotze Bursary) and top ups by my supervisors.

I would like to thank my research team members, Prof. Charles H. Stirton for his cheerful comments and suggestions that significantly improved the thesis. Dr Samson BM Chimphango for his advice and support.

I thank my Journal club members and lab-mates in both Verboom's and Muasya's groups, Dr. Nicola Bergh, Dr Meshack N. Dludlu, Seth Musker, Zaynab Shaik, Klara Beckerling, Ruan Van Mazijk, Maria Yakubu, Dunja MacAlister, Rhoda Adaramola, Dr. Tammy Elliott, Graham Duncan, John Kimeu, Ngalirendwe Muthaphuli, Tonny Selinga, Lara Wootton, Muneiwa Tshikuvhe, Givemore Makonya and Zoe Poulsen for the stimulating discussions and all the fun we have had in the fields and in the laboratory over the last three years.

I thank Petra Muller, Gonzalo Aguilar, Boitumelo Marope, Bongani Tom, Desmond Barnes and Dr Dawood Hattas for technical support. Claire Khai, Soraya Abrahams, Jamie-Lee Cupido and Andrea Plos in the Department of Biological Sciences, UCT are thanked for logistical support..

The curators and staff of herbaria, BOL (Mr Terry Trinder-Smith, Dr Cornelia Klak and Charlene Christian), FHI, FHO, K (Dr Martin Cheek, Harry J. Smith, etc), NBG (including SAM and STE), OXF and PRE for allowing access and loan of materials and their hospitality during research visits.

Last, but surely most importantly, I thank my wife, Dmmagi Daniel Zhigila for her immense support, taking care of the family while I was away for this study. My kids, Galinah and Capstone for growing without me for this period.

**Abstract**

*Thesium* L. (Santalales: Santalaceae) is a large (360 species) genus of hemiparasitic perennial or annual species with a mainly Old-World distribution and a greatest concentration in southern Africa (*ca*. 186 species). Although *Thesium* is a major component of southern African flora, it often goes unnoticed and is poorly studied. The last revision of the entire genus was done by De Candolle in 1857. South African *Thesium* was last revised by Hill almost a century ago. Since Hill's revision, the number of collections have grown, and 49 new species have been described. Currently, no comprehensive *Thesium* taxonomic key exists, and species delimitation remains difficult due to a high variation in character states, rendering the genus in need of major revision. Within southern Africa, *ca*. 103 species occur in the Greater Cape Floristic Region (GCFR), of which about 72 are regional endemics. The GCFR *Thesium,* including ecological specialists and generalists, offers an appropriate system for evaluating both the correlates of range extent, specialisation and the relative extinction risks associated with both ecological strategies. Here, it is predicted that a combination of edaphic, elevation and climate variables influence the geographic range of *Thesium* in the GCFR.

Recent phylogenetic hypotheses revealed that *Thesium* is paraphyletic with respect to *Austroamericium, Chrysothesium, Kunkeliella* and *Thesidium,* suggesting the need for generic realignment. In addition, existing subgeneric and sectional classifications of this large genus lack a phylogenetic basis, thus compromising their predictive value. Using an expanded taxon sampling and a combination of nuclear (ITS) and chloroplast (matK, rpl32-trnL and trnL-F) DNA sequence data, chapter two re-assesses the phylogenetic relationships of *Thesium* and uses these as the basis of a new subgeneric classification of the genus. The phylogeny obtained confirms the need to place the four segregate genera into synonymy, resulting in a monophyletic *Thesium*. In addition, it resolves five, well-supported major clades within *Thesium* which I recognize as subgenera. The South African endemic subgenus *Hagnothesium* is sister to the Eurasian subgenus *Thesium* (including *Thesium, Kunkeliella* and *Mauritanica*). The subgenus *Psilothesium,* occurring in tropical South America (formerly genus *Austroamericium*) and tropical Africa, is sister to the rest of the subgenera, which are all confined to South Africa. Within the latter, the subgenus *Discothesium* consists of subtropical and temperate species, whereas subgenus *Frisea*, comprising previously recognized sections *Annulata, Barbata Frisea*, *Imberbia* and *Penicillata*, is restricted to the GCFR. To facilitate identification of subgenera, I present identification keys, assigned species, provide brief diagnoses, identified ancestral morphological characters and, supply distribution and ecological

data.

*Thesium* subgenus *Hagnothesium* is endemic to the GCFR. In the past, there has been a propensity in revisionary work of the subgenus *Hagnothesium* to split taxa into distinct species or *vice-versa*. Consequently, 15 different names exist although only six are accepted formally. Following recent molecular phylogenetic studies, the monophyly of the subgenus *Hagnothesium* is now well-established, but the circumscription of species within the section remains problematic given the complicated nomenclatural history which has added further confusion. Chapter three presents a revision of subgenus *Hagnothesium* using a total evidence approach to propose a modern taxonomy. I studied both herbarium collections and plants in their natural populations to circumscribe species boundaries, geographical ranges and estimates of their conservation status. Species of the subgenus *Hagnothesium* are dioecious, generally having four- merous, campanulate flowers, spikes borne in bract axils and arranged along the length of branchlets, with valvate perianth lobes and a short to absent hypanthial tube. The following eight species were recognized, of which one is here described as new: *T. fragile* L.f., *T. fruticulosum* (A.W.Hill) J.C.Manning & F.Forest, *T. hirtum* (Sond.) Zhigila, Verboom & Muasya *comb. nov., T. leptostachyum* A.DC., *T. longicaule* Zhigila, Verboom & Muasya *nom. nov., T. microcarpum* A.DC., *T. minus* (A.W.Hill) J.C.Manning & F.Forest and *T. quartzicolum* Zhigila, Verboom & Muasya *sp. nov*. I provide updated taxonomic keys, species descriptions, illustrations, distribution maps, new combinations, synonyms, and notes on the red list status for each species.

In addition, six new species of *Thesium* endemic to the GCFR (but not included in subgenus *Hagnothesium*) are described and illustrated in chapter four. These are: *Thesium aspermontanum* Zhigila, Verboom & Muasya *sp. nov., T. dmmagiae* Zhigila, Verboom & Muasya *sp. nov., T. neoprostratum* Zhigila, Verboom & Muasya *sp. nov., T. nigroperianthum* Zhigila, Verboom & Muasya *sp. nov., T. rhizomatum* Zhigila, Verboom & Muasya *sp. nov.,* and *T. stirtonii sp. nov.* Also, *Thesium assimile* var. *pallidum* is elevated to species rank as *T. sawae* Zhigila, Verboom & Muasya *stat. nov.* Morphological and ecological differences between species, along with their putative affinities, preliminary conservation status, phenology, etymology and distributional maps are presented.

Narrow-ranged species are expected to be more at greater risk of extinction than generalists due to climate change. Such risk is greatest in biodiversity hotspots such as the GCFR, which

house both ecological specialists and generalists. It was hypothesized that range size, ecological specialization and consequent climatically-modulated extinction-risk are all phylogenetic structured, such that climate change will precipitate a disproportionate loss of phylogenetic diversity. Past and future species distribution ranges were developed using MaxEnt models based on present-day occurrences and environmental conditions. There was a strong positive correlation between the ecological niche breadth of species, as determined by large-scale environmental variables, and their range extents. One hundred and one *Thesium* species were modelled, of which 71 species (83%) were predicted to have had broad range sizes during the Last Glacial Maxima, and 27 species (17%) recorded range contractions historically to the present. Similarly, 45 species (44%) will potentially expand their ranges, while 51 species (50%) are predicted to reduce their ranges in the future. Of the 65 species currently ranked as Least Concern or Data Deficient in the South African Red list, 24 species will likely shift into higher extinction risk categories. Interestingly, five ecological specialists (5%), although having experienced a range reduction from the LGM to the present, are predicted to persist in the face of future climate change. However, the range extent, ecological specialisation and extinction risk are phylogenetically random and therefore should have a negligible impact on the phylogenetic diversity of the GCFR *Thesium.*

Overall, this study confirms the monophyly of the genus *Thesium* and sets its infrageneric classification scheme in place. The context of this classification framework allows the systematic revision of the genus, one clade at a time. Towards this goal, I revised the *Hagnothesium* clade and additionally described six new species from other clades. The climate, elevation and soil variables influence the distribution range and specialism of GCFR *Thesium* clades. However, ecological specialism of species and extinction risks were predicted to be phylogenetically random.

## Table of Contents

**LIST OF FIGURES**

**LIST OF TABLES**

**LIST OF APPENDICES**

# CHAPTER ONE

## 1.0 GENERAL INTRODUCTION

### 1.1 Etymology and distribution of *Thesium*

*Thesium* is a genus of the family Santalaceae (The Angiosperm Phylogeny Group IV, 2016), also called Thesiaceae (sensu Nickrent and Der, 2010), in the tribe Thesieae. *Thesium* is derived from the Latin, *thesion* that translates to "bastard toad flax" used by Plinius. It stems from the Greek *thēseion*, probably from neuter of *thēseios* of Theseus, or from the *Thēseus* (Theseus), a mythological Greek hero (Skeat, 1910). According to some authors, the genus was named after Theseus, a hero of Attic legend, son of Aegeus, King of Athens and Athera, daughter of Pitteus, King of Trozeon. The Greek word Theseion means "The Temple of Theseus" (Merriam-Webster, 2019).

*Thesium* is a species-rich genus in the order Santalales, with *ca*. 360 species occurring worldwide (Nickrent and García, 2015; The Plant List, 2019). Species in the genus *Thesium* are hemiparasites (Nickrent and Der, 2010). Over one third (*ca*. 190 species) are found in South Africa and most of these occur in the Greater Cape Floristic Region (GCFR) (Romo et al., 2004; Manning and Goldblatt, 2012; Snijman, 2013; Nickrent and García, 2015; García et al., 2018; Visser et al., 2018; Fig. 1.1). Although *Thesium* is a common and abundant component of the vegetation of southern Africa, especially in the Fynbos Biome (Manning and Goldblatt, 2012), it often goes unnoticed on account of its drab morphology.

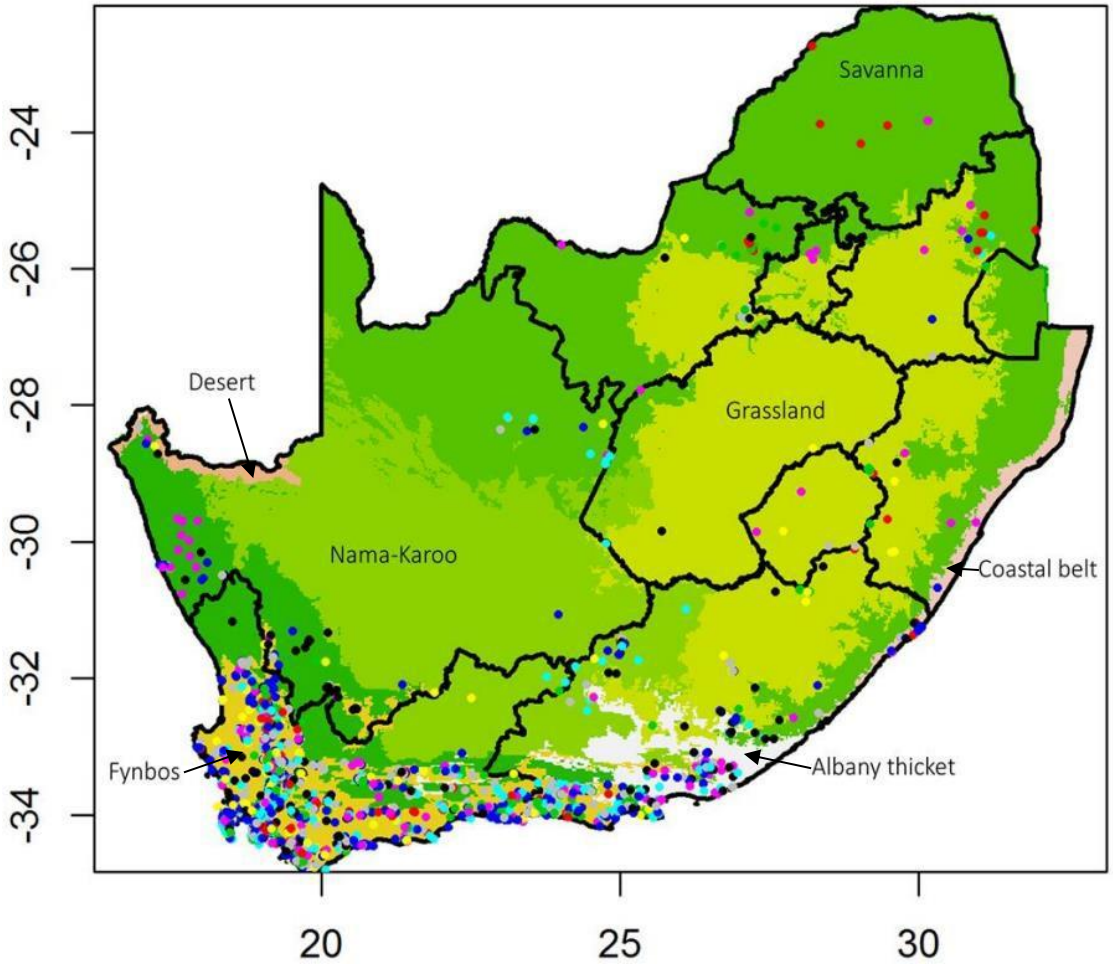



**Fig. 1.1:** Occurrence of South African *Thesium* species based on georeferenced herbarium specimen data. The major biomes are shown in different major shade of green to white. Unique coloured dots represent different species, to show species diversity across the South African biomes.

### 1.2 Morphology of *Thesium.*

*Thesium* plants are annual herbs and perennial shrubs or shrublets (Linnaeus, 1753; Der and Nickrent, 2008). They exhibit a complex and wide variation in habit, vegetative morphology, reproductive morphology and habitat (Fig. 1.2A–I). However, most species are small in stature, < 50 cm tall (Hill, 1925; Zhigila et al., 2020). The basal portion of the plant may be stoloniferous, rhizomatous, or may form a caudex from which numerous vertical shoots arise (Hill, 1915). Stems may be sparsely to densely branched, fastigiate, or virgate and can be terete, costate or alate in cross section (Lombard et al., 2019). The stem is diverse in colour, ranging from yellow, through golden or greyish, to green. The foliar organs are alternate or more rarely opposite, typically decurrent or sessile and range from lanceolate to linear and minute scales to almost lacking (Hill, 1915). Inflorescence types are extremely variable among the species, but all can

be viewed as derived from a cymosely-branched panicle. Various degrees of reduction can result in inflorescences that superficially resemble racemes and spikes, but upon closer inspection, these types are basically dichasial in composition (Der and Nickrent, 2008). The minute flowers are unisexual or bisexual and range from white to greenish. Generally, flowers are subtended by two bracteoles (bractlets) and two bracts. In some cases, such as *T. ebracteatum*, bracteoles are lost entirely. In squamate *Thesium* species, floral bracts grade gradually into vegetative scale leaves (Visser et al., 2018). *Thesium* inflorescences can also exhibit recaulescence (Weberling, 1989), where the position of axillary floral buds is shifted owing to stretching of the common basal portions of the pedicel and subtending peduncular branch. Such processes lead to many intermediate versions of inflorescence types and can complicate interpretation. Flowers are generally 5-merous and monochlamydous (with one perianth whorl). In literature, this whorl is referred to as the corolla, perigonium, tepals, or perianth (García et al., 2018). However, it is in this study interpreted as the perianth following Hill (1915). The nut-like fruits in *Thesium* provide several taxonomic characters that have previously been used to differentiate groups, particularly venation on the exocarp (reticulate vs. longitudinal). The withered perianth may remain attached to the apex of the mature fruit and it may be long or short (correlated with original perianth and hypanthium tube lengths). In many *Thesium* species, the pedicel of the flower enlarges upon fruiting to form an elaiosome (Zhigila et al., 2020). This structure is attractive to ants, which remove and disseminate the fruits by myrmecochory (Gorb and Gorb, 2003). Hendrych (1972) associated myrmecochory with short distance dispersal, but he clarified that other mechanisms may also play an important role.

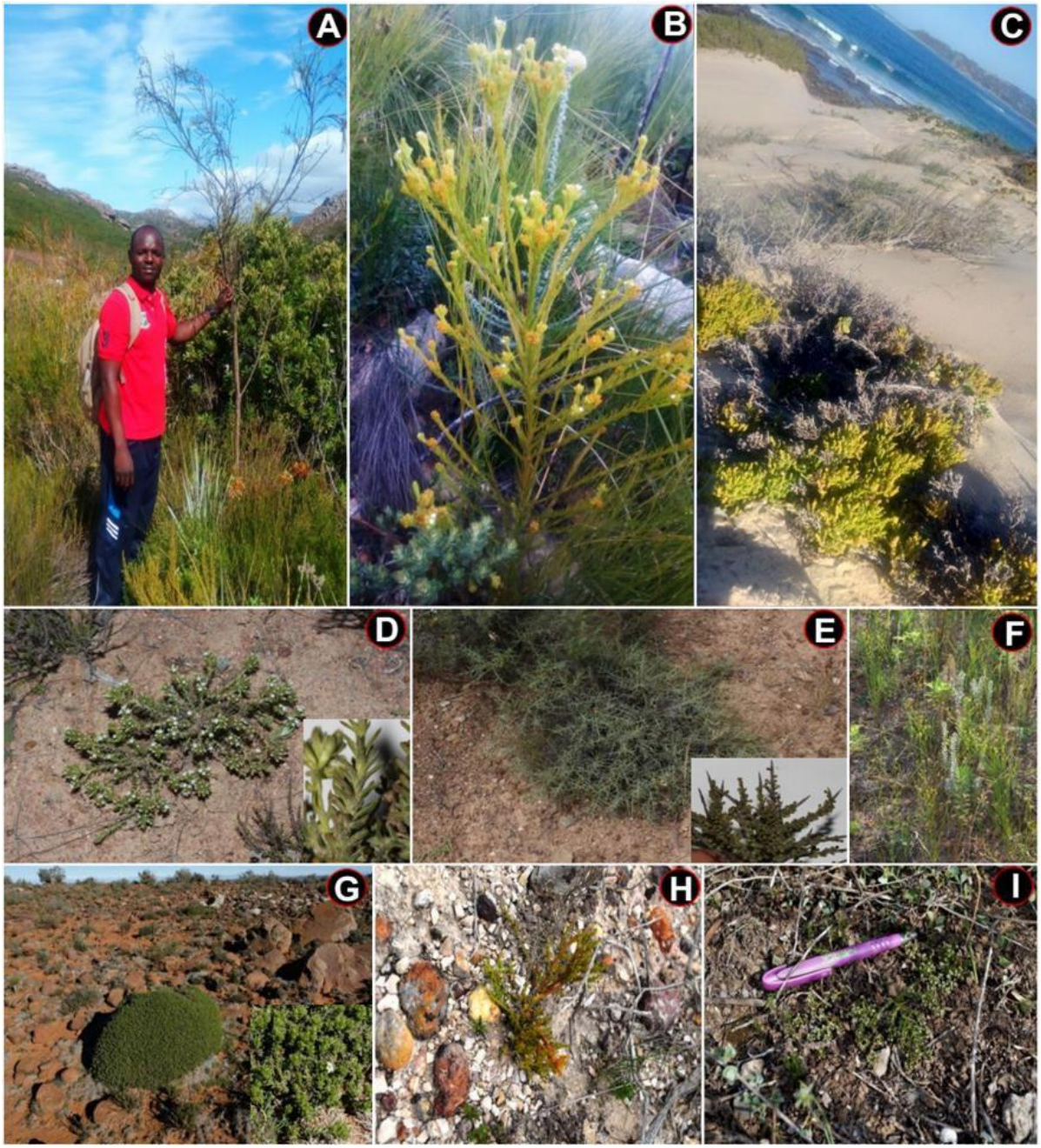



**Fig. 1.2:** Diversity in growth form, habitat and morphology of the South African *Thesium* A) *T. pycnanathum* tall (up to 2.5 m tall), erect occurring along stream sides; B) *T. carinatum*, < 50 cm tall, with a virgate branching pattern, mostly on sandstone-derived soil, C) *T. fragile*, occurring on beach sand; D) *T. hispidulum*, a heath-like decumbent shrub, on arid soil; E) an intricate branching pattern in *T. hystrix*; F) an erect, slender habit in *T. virgatum*; G) a mounded growth form in *T. imbricatum*; H) *T. quartzicolum* on quartz-silcrete soil; I) *T. rhizomatum*, a short (< 8 cm tall) plant on alluvial sand. Photos D and E by Brian du Preez, F by Charles H. Stirton, G by Nick Helme and the remainder by Daniel A. Zhigila.

### 1.3 The GCFR as the center of *Thesium* diversity

The GCFR is located at the Southwest corner and southernmost part of the African continent and the confluence of the Indian and Atlantic oceans (Goldblatt, 1978). The region lies between latitude 28–35° S and longitude 18–26° E. It is characterized by wet winters and intense summer drought (Mediterranean climate), with a historically stable climate and is highly fire-prone (Midgley et al., 2003, Allsopp et al., 2014). The GCFR comprises five major vegetation types, namely Fynbos, Renosterveld, Succulent Karoo, Forest and Thicket, each controlled by different environmental variables (Mucina and Rutherford, 2006; Allsopp et al., 2014; Bergh et al., 2014). Plant substrates are substantially variable in the GCFR (Cramer et al., 2014), including: shale, sandstone, quartz, granite, calcareous substrata, alluvial deposits, and acid lowland sand (Allsopp et al., 2014). These mosaic ecological niches of the GCFR are probably responsible for the spectacular species richness and diversity in comparison with similar biomes in other regions of the world (Mucina and Rutherford 2006, Manning and Goldblatt, 2012; Allsopp et al., 2014; Verboom et al., 2015). The GCFR (comprising the Core Cape Region and the Extra Cape Region) has about 11 423 vascular plant species in an area of ~189 000 $km^2$ of which ca 78% are endemic (Manning and Goldblatt, 2012; Snijman, 2013; Allsopp, 2016). Like in other biomes of southern Africa, local endemism is very high (Van Wyk and Smith, 2001), but the cause(s) of radiation in diversity and endemism is still unclear (Allsopp et al. 2014). Evidently, geological and environmental heterogeneity (diverse edaphic factors, climatic variables and topography) are linked to this remarkable hyper-diversity. Harrison and Noss (2017) linked the geographical pattern of endemism hotspots to stable climatic variables over time. This inference agrees with many other interpretations of endemism of plants *e.g.* Noss et al. (2015) and Feng et al. (2019). Thus, the GCFR is often used to invoke hypotheses on the contribution of an environmental heterogeneity continuum on the origin and distribution of biodiversity (Schnitzler et al., 2011). Hence, the GCFR has been identified as a model system for the analysis of plant diversification and speciation on the continent (Born et al., 2007; Dreyer et al., 2009).

*Thesium* is widely distributed in the GCFR, occurring on all major substrates, although it seems to favour sandstone-derived soils (Manning and Goldblatt, 2012). The flowering time varies within *Thesium*, particularly among the GCFR species. The peak of flowering is between August and January, while the fewest species flower around May (Manning and Goldblatt, 2012; Fig. 1.3).

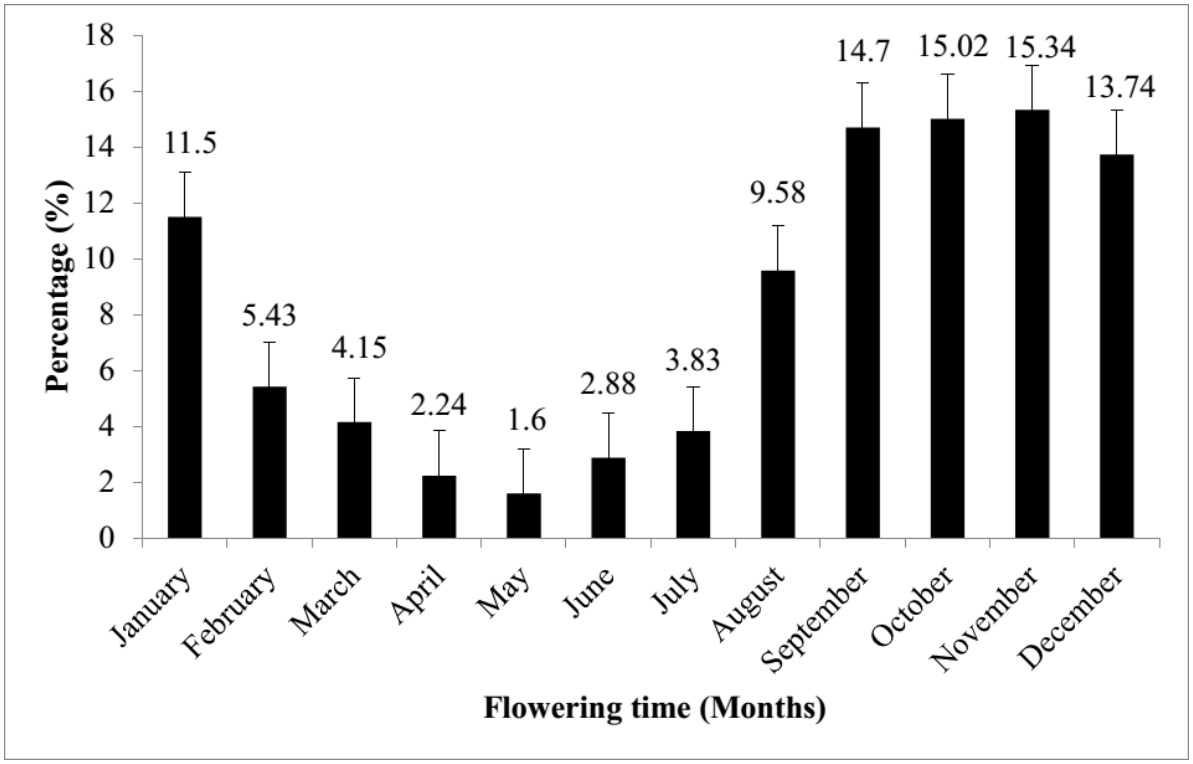



**Fig. 1.3:** Flowering time of the GCFR *Thesium* species. The peak of the flowering period is between August and January. The fewest species flower between March and July with the least flowering in May (1.6% species). Data from (Manning Goldblatt, 2012; SANBI, 2019; Zhigila et al., 2019a).

### 1.4 Potentials of morphometrics and phylogenetic analyses

Despite the increasing rate in use of molecular evidence to defined taxa, morphology remains a fundamental criterion in systematic biology (Koutecký, 2015). The "Orthodox and Natural groups", based on overall similarity (phenetic relationship), have long been the basis for plant classifications (de Jussieu, 1774) and understanding of phylogenetic relationships (Savriama, 2018). Interestingly, the use of multivariate morphometrics has developed rapidly over the last 35 years in a variety of disciplines (Hernderson, 2006; Koutecký, 2015), including systematics (Henderson, 2006; Savriama, 2018). Importantly, the proliferation of computational software packages *e.g.* Statistica (Tibcom, 2018), PAST (Hammer et al., 2001) and R (Core Team 2019) in recent years have aided the improvement in the power of multivariate morphometrics (Koutecký, 2015). This approach to delimit species remains valid if the technique captures the geometry of morphological structures and reinvigorates the traits with bivariate or multivariate analysis (Wiley and Lieberman, 2011, Savriama, 2018). Morphological characters of plants have provided the foundation and framework for taxonomy and they have been used extensively in the preparation of classification systems, diagnostic keys, etc. (Cope et al.,

2012). Also, the formal description and diagnosis of species is based heavily on morphological illustrations (Rohlf and Marcus, 1993). These suggest the validity of morphological traits as taxonomically informative characters.

Additionally, in recent years the molecular-based approach has begun to dominate. However, traditional methods (Linnaean taxonomy) of plant taxonomy based upon comparative external morphological and anatomical characters are still indispensable to systematics. This traditional method continues to predominate and has a bigger influence over other sources of taxonomic characters in plant classification mainly due to: i) morphological characters are easily observable and measurable, since they have innumerable variants, they help in delimitation, to identifying species and their relationships (Cope et al., 2012); ii) To analyze morphological characters, one does not need sophisticated laboratory arrangements (Clark, 2007). A hand lens or dissecting microscope, or possibly a light microscope is enough to study these characters (Bruno et al., 2010); iii) there is a well- knit terminology to describe the variations as morphological characters that have been in use for plant classification for several centuries (Cope et al., 2012); iv) the time and effort needed to obtain information from other sources such as phytochemistry and molecular biology ensure the advantage of morphological characters over others in plant taxonomy (Zhigila et al., 2015); v) the advent of high-quality digital cameras and sophisticated smart phones that are designed to allow users in the field to photograph specimens of interest and instantly receive information about them have become ubiquitous, increasing interest in creating hand-held field guides. Ultimately, morphological characters help to define taxa more effectively by providing fast, practical-based plant identifications particularly for citizen scientists.

Although phylogeny based on morphological data is well-established and a broad discipline, morphological traits alone present some specific challenges (Stevens, 1991, Cope et al., 2012). These include, among others, the effects of the environment on plants (plasticity), species adaptive behaviors, specimen deformations, methods of discrete quantitative character coding (Stevens, 1991), unclear class boundaries, and trait selection and terminology. Indeed, there is no single method that can provide a panacea for all taxonomic circumscriptions, therefore appropriate methods need to be chosen for each undertaking at hand (Cope et al., 2012). Recently, molecular phylogenies have become increasingly available for species identification and have made species classification fast, reliable and accurate. Notwithstanding, molecular information alone was insufficient to completely resolve the relationships within some genera *e.g. Santalum* L. (Santalaceae; Harbaugh and Baldwin, 2007; Harbaugh, 2008). For this study, in addition to expanded phylogenetic analyses based on molecular sequences, biogeographic

pattern was integrated with morphological characters.

### 1.5 Models of geographic distribution of species

*Thesium* is more diverse in the GCFR than anywhere else in the world (Moore et al., 2010; García et al., 2018; Zhigila et al., 2020). The drivers of this diversification can be predicted from the heterogenous environmental conditions associated with the GCFR (Manning and Goldblatt, 2012; Verboom et al., 2014). Exploring relationships between each species and the environment will help understand which variables are most important in predicting its habitats. Developing predictive distribution models allows one to generate potentially new geographic range maps showing where in the landscape the most suitable conditions for species occur. If predictions are probabilistic habitats, then predictions are only good if they reflect the actual occurrences of species (Guisan and Zimmermann, 2000; Chivers et al., 2014). Hence, understanding the correlates of why species occupy their geographic distribution ranges remains a cornerstone of macroevolution and biogeography.

In every province of South Africa, particularly in the Western Cape, Nature Reserves have been set aside as protected areas designated for conservation and recreation (IUCN, 2017), but interrogating other places at risk outside those reserves provides insight into the potential of conservation investment in those areas (Pressey et al., 2007; Mora and Sale, 2011). In some cases, the ecological niche models propose that reserved areas may no longer sustain populations of red listed species, probably the very ones that the reserves were created to care for (Marini et al., 2009; Thorn et al., 2009). Generating distribution maps at finer scale resolution provides conservation intelligence for better and smarter hypotheses to these questions and ultimately to guide conservation actions (Phillips et al., 2006; Lirio et al., 2015; Phillips et al., 2017; Villero et al., 2017; Urbina-Cardona et al., 2019).

Species Distribution Models (SDMs) have proven valuable for envisaging the possible distribution of species by relating their occurrences to environmental variables (Keppel et al., 2017; Urbina-Cardona et al., 2019). This could be the reason why ecological niche models (ENMs) have become progressively more popular tools for predicting the ecological ranges of species (Rangel and Loyola, 2012) and have been used for the management of nature reserves (Kremen et al., 2007; Lozier et al., 2009; Urbina-Cardona et al., 2019), and for assessment of speciation patterns and niche difference (Warren et al., 2008). Species populations can then be predicted by combining the possibilities of individual species models (Dubuis et al., 2013). Topographical elements and biotic interactions such as climate, soil and disturbance are pivotal factors in determining the range size of plant species – and hence, inform species occurrence,

range size and distribution (Dexter et al., 2012, Souza et al., 2013; Perret et al., 2006; Elith and Leathwick, 2009; Lirio et al., 2015; Saiter et al. (2016). In addition, strong correlations between species climatic ranges and various ecological variables have been demonstrated with strong relationships (Toledo et al., 2012; Qian, 2013; Rezende et al., 2015; Saiter et al., 2016). This suggests that climatic factors drive species biogeographical shifts, especially at higher elevations (> 600 m) (Saiter et al. 2016). According to Keppel et al. (2017), climatic factors and geomorphological variables could suggest strong and useful predictors and indicators of ecosystem diversity. According to Elith and Leathwick (2009), the use of SDMs is one of the most important tools in conservation strategies, especially with respect to climate change. This aids the evaluation of present and potential future species range sizes relative to geoclimatic variables, soils and other environmental predictors. These models can highlight species that perhaps will be at risk of extinction from climate change (Thuiller et al., 2005), and habitats that may face significant shifts in diversity and species composition (Williams et al., 2005; Iloh and Ogundipe, 2016).

### 1.6 Statement of the problem

Since Linnaeus (1753) established the taxonomy of *Thesium*, it has enjoyed the attention of several taxonomists, including Hill (1915a) to Hendrych (1972), with Hill's work providing the most comprehensive taxonomic review of the southern African species to date. Since then, more fieldwork has added materials and blurred the taxonomy, with over 40 species of the GCFR lineages having a conservation status of Data Deficient due to unclear taxonomy (SANBI, 2015). Subsequent phylogenetic works (Der and Nickrent, 2008; Moore et al., 2010; Nickrent and García, 2015) have built on these early studies, providing an assessment of the monophyly of the genus and its component sections, and providing an initial estimate of species-level relationships. Notwithstanding these advances, several taxonomic/systematic challenges remain. Foremost amongst these are that many species remain difficult to key out, a clear indicator of the need for a comprehensive taxonomic revision, and that the best available phylogenetic hypotheses (Moore et al., 2010; Nickrent and García, 2015) are insufficient, in terms of completeness and resolution, to provide a solid foundation for a new sectional classification. Rightly, the South African National Research Strategy listed *Thesium* as one of the genera in need of taxonomic revision (Victor et al., 2015). Recently, Visser et al. (2018) revised the *T. goetzeanum* species complex. Of the 16 accepted species names (The Plant List, 2017) only nine were recognized as distinct species. This highlights the need for a taxonomic revision of the entire genus, particularly the GCFR species. Hence, a robust monophyly-based

sectional classification is essential for the revision of a genus of this size. Also, within the GCFR *Thesium* has both narrow-ranged and wide-ranged species that could be used as models to explore the correlates of geographic range limits, ecological specialisation and the relative extinction risks faced by narrowly-endemic versus widespread species in the face of accelerating climate change.

### 1.7 Rationale and aims

The thesis focuses on the genus *Thesium*, employing an approach that integrates taxonomic and systematic methodologies with species distribution modelling. The following are the overall goals of the study, each leading to a distinct chapter:

(i) to develop an infrageneric classification based on robust morphological and molecular phylogenetic framework;

(ii) to revise the taxonomy of the *Hagnothesium* clade.

(iii) to describe putative new species within other clades.

(iv) to develop distribution models for the GCFR clade species and use these to assess whether range size variations, ecological specialisation and extinction risks are phylogenetically non-random and, therefore, whether extinction is likely to impact *Thesium* phylogenetic diversity.

### 1.8 Structure of the thesis

The first chapter presents a general introduction and the objectives of the thesis.

Chapter two sets out to test hypotheses on the monophyly of the genus with respect to the previously segregated genera *Thesidium, Kunkeliella* (Forest and Manning, 2013) and *Austroamericium* (Hendrych, 1963; Nickrent and García, 2015). Moore et al. (2010) used ITS and trnL-F sequences to initiate molecular-based phylogenetics of species in the genus. In this study, I sampled additional loci and taxa to i) establish a sufficiently well-resolved phylogenetic hypothesis for the genus *Thesium*, (ii) to propose an infrageneric classification framework within the context of the molecular phylogeny, and (iii) informed by the monophyly of each clade, to map relevant geographical patterns and morphological characters on the phylogeny with the view of identifying diagnostic morphological characters for each clade. Then, I used these traits to build a taxonomic key and present a diagnosis to delineate each proposed clade.

Informed by the phylogenetic relationships obtained in chapter two, and identification of the monophyletic *Hagnothesium* clade as most in need of urgent taxonomic revision, chapter three presents a formal taxonomic circumscription of species within this clade. The

International Plant Names (2019) listed 15 species names in this clade, but only six were accepted. Adopting the unified species concept (de Queiroz, 2007) and the use of multivariate morphometric analyses (Koutecký, 2015), I recognise eight distinct clusters (*T. fragile, T. fruticulosum, T. hirtum, T. leptostachyum, T. longicaule, T. microcarpum, T. minus* and *T. quartzicolum*) as species; of which only *T. quartzicolum* was undescribed. In addition, identification of specimens collected during the study resulted in some further taxa being new to science. Chapter four pursues the formal taxonomic descriptions of these collections. These are *Thesium aspermontanum* Zhigila, Verboom & Muasya, *T. dmmagiae* Zhigila, Verboom & Muasya, *T. neoprostratum* Zhigila, Verboom & Muasya, *T. nigroperianthum* Zhigila, Verboom & Muasya, *T. rhizomatum* Zhigila, Verboom & Muasya and *T. stirtonii* Zhigila, Verboom & Muasya. *Thesium carinatum* DC var. *pallidum* (Sond.) A.W.Hill was elevated from a variety status to the species *T. sawae* (A.W.Hill) Zhigila, Verboom & Muasya.

Chapter 5 (i) tests the hypotheses that species range sizes are associated with its responses to environmental variables. Changes in environmental variables due to global warming are believed to impact negatively on specialists, while generalists are believed to respond positively to this disturbance (Vazquez and Simberloff, 202); (ii) predict species habitat suitability through time (past, present and future) and estimate change in range sizes; and (iii) within a phylogenetic context, to test hypotheses that species at greater risk of extinction are closely related and that the threats will likely impact the phylogenetic diversity of *Thesium*. The final chapter presents a synthesis of this thesis.

# CHAPTER TWO

## 2.0 An infrageneric classification of *Thesium* (Santalaceae) based on molecular phylogenetic data

### 2.1 INTRODUCTION

Taxonomic studies of *Thesium* date back to Linnaeus (1753) who erected the genus, and recognized four species, *T. alpinum* L., *T. capitatum* L., *T. linophyllon* L. and *T. umbellatum* L. Following the description of several additional species by Linnaeus' son (Linnaeus, 1782) and others (*e.g.* Nuttal, 1818), Reichenbach (1828) presented the first infrageneric classification, proposing the segregation of *Thesium* into three sections, *Euthesium* Benth. (= *Thesium* L.), *Thesiosyri* Endl. and *Frisea* Endl. on the basis of distribution and reproductive traits. Subsequently, Jaubert and Spach (1844) established section *Chrysothesium* to accommodate two newly-described species from Turkey, and section *Psilothesium* to accommodate the South American species. This was followed by the work of De Candolle (1857a) who described 112 species and proposed a classification with five sections: *Aetheothesium* DC., *Discothesium* DC., *Euthesium, Frisea* and *Hagnothesium* DC. Although Sonder (1857a), having described about 25 species, segregated *Hagnothesium* from *Thesium* to recognize a distinct genus *Thesidium* Sond. based on flower unisexuality, he (Sonder, 1857b) reverted to the classification of De Candolle (1857b) within the same year, reducing *Thesidium* to a section. De Candolle's (1857b) infrageneric classification was adopted by a series of subsequent taxonomic treatments (*e.g.* Hieronymus, 1889; Kuntze, 1904).

Hill (1915a, 1925) produced a major taxonomic revision of South African *Thesium*, based on vegetative and floral morphology, recognizing 128 species and erecting four sections: *Annulata* A.W.Hill, *Barbata* A.W.Hill, *Imberbia* A.W.Hill (subsections *Fimbriata* A.W.Hill and *Subglabra* A.W.Hill) and *Penicillata* A.W.Hill, and treating *Thesidium* (eight species) as a separate genus. This work provided a foundation for the work of Pilger (1935) who produced the first treatment considering species from across the full distribution range of the genus. Pilger recognized four sections within *Thesium*, *Frisea* (including subsections *Annulata, Penicillata* and *Barbata*), *Chrysothesium, Psilothesium* and *Euthesium*, while continuing to treat *Thesidium* as a distinct genus. In 1936, Bobrov presented a detailed infrageneric taxonomy for the Eurasian species, in which he divided *Euthesium* into two sections: *Thesium,* with several series, and, *Macranthia* Bobrov. Hendrych (1963; 1972) thereafter produced the most comprehensive taxonomic review of *Thesium* to date. His work incorporated detailed

discussions of morphology, taxonomy, and hypothesized subgeneric/generic phylogenetic relationships. Subsequent to this work, the Canary Islands endemics, *T. canariensis* (W.T.Stearn) J.C.Manning and F.Forest, *T. psilotocladum* Svent, *T. retamoides* (A.Santos) J.C.Manning and F.Forest and *T. subsucculentum* (Kämmer) J.C.Manning and F.Forest were segregated as a separate genus – *Kunkeliella* Stearn (Stearn, 1972), while Hendrych (1994) established a new genus, *Austroamericum* Hendr. to accommodate the South American species previously included in section *Psilothesium*. In addition, Hendrych (1994) elevated the Eurasian section *Chrysothesium* to subgenus following his description of several new Eurasian species. Although the South African and tropical African sections are listed in these treatments, the large groups (*e.g.*, section *Imberbia* subsection *Subglabrata* containing *ca*. 75 species and section *Barbata* containing *ca*. 90 species), which make up the bulk of species in the genus, have received little attention subsequent to the work of Hill.

Since the 1980s several checklists and floras have been published that contain regional treatments of *Thesium*; *e.g.* for Iran (Polatschek, 1982), Egypt (Sa'ad, 1983), Pakistan (Nasir, 1984), Central Africa (Lawalrée, 1985), Ethiopia (Miller, 1989), South Tropical Africa (Hilliard, 1991; Hilliard, 2004), China (Shu, 2003), Crimea (Romo et al., 2004), Tropical East Africa (Polhill, 2005), Madagascar (Rogers et al., 2008), Nigeria (Hutchinson et al., 2014), Lithuania (Gudžinskas and Žalneravičius, 2017) and Zimbabwe (Hyde et al., 2017). In addition, Mashego and Le Roux (2018) published a short communication on the southern African taxa. Recently, Visser et al. (2018) and Zhigila et al. (2019a) revised the *T. goetzeanum* species complex of the grassland and section *Hagnothesium* of the Greater Cape Floristic Region (GCFR), respectively. Although these regional treatments of *Thesium* have added to our understanding of the global diversity of the genus, a subgeneric classification based on phylogenetic relationships remains lacking.

Since it is widely appreciated that a phylogenetic basis improves both the stability and predictiveness of supraspecific classification (Dayrat, 2005; Humphreys and Linder, 2009; Duminil et al., 2012; Judd et al., 2012; Mitchell et al., 2017), there is an urgent need to integrate phylogenetic information in the subgeneric and sectional classification of *Thesium*. The first molecular-phylogenetic study of Santalaceae (Der and Nickrent, 2008) provided a basis for the inclusion of six genera, *Thesium, Kunkeliella, Thesidium, Osyridocarpos* DC., *Buckleya* Torr., and newly-described (Nickrent and García, 2015) *Lacomucinaea* Nickrent and M.A.García in a segregate family Thesiaceae (sensu Nickrent et al., 2010). A subsequent study (Moore et al., 2010), utilizing plastid (trnL-F intergenic spacer) and nuclear (ITS) gene markers, and focusing on the phylogenetic relationships of South African *Thesium*, found *Thesium* to be paraphyletic

with respect to *Austroamericium*, *Chrysothesium* and *Thesidium*, and accordingly suggested the need for generic realignment. Thus, informed by this phylogenetic evidence, Forest and Manning (2013) sank *Thesidium a*nd *Kunkeliella* into *Thesium*. The infrageneric classification of *Thesium* is, however, still hampered by a lack of phylogenetic resolution, with previous studies relying on just a few DNA markers and incomplete taxonomic sampling. Hence, the placement of many taxa remains uncertain and our knowledge of phylogenetic relationships has been insufficient for the development of a reliable infrageneric classifications.

Clearly, an expanded phylogenetic sampling of both DNA loci and *Thesium* species is needed to provide a sound basis for its infrageneric classification. Here, I make use of DNA sequences from the nuclear (ITS) and chloroplast genomes [matK, rpl32-trnL(UAG) and trnL-F], which are standard sources of phylogenetic information at the infrageneric level (*e.g.* Wang et al., 2004), with ITS and trnL-F being applied previously to *Thesium* (Moore et al., 2010) or Thesiaceae (sensu Nickrent and García, 2015). The objectives in this study were: (i) to develop a robust phylogenetic hypothesis for *Thesium* based on additional DNA markers andsampling complete GCFR species; (ii) to use this phylogenetic framework as the basis of an infrageneric classification in which taxa are monophyletic; and (iii) to optimize morphological characters on the phylogenetic tree for the purpose of identifying ancestral morphological characters of the various infrageneric taxa, thereby facilitating diagnosis.

## 2.2 MATERIALS AND METHODS

**2.2.1 Taxon and gene sampling. –** One hundred and sixty targeted accessions, representing 116 *Thesium* species and four markers [ITS, matK, rpl32-trnL(UAG) and trnL-F], were sampled. This substantially expands the species-level molecular phylogenetic sampling of *Thesium*, particularly of species from the Core Cape Subregion (CCR) of the GCFR (Manning and Goldblatt, 2012; Snijman, 2013). The new sequences were added to existing data sets comprising all previously-published nuclear (ITS, 114 accessions) and chloroplast (trnL-F, 87 accessions; matK, 12 accessions) sequences of *Thesium*, along with representative sequences of *Lacomucinaea lineata* (L. f.) Nickrent & M. A. García, *Buckleya distichophylla* Torr., and *B. lanceolata* Miq., which were included to root the resulting trees. The outgroups were chosen on the basis of their placement in previous phylogenetic analyses (Moore *et al*., 2010; Nickrent and García, 2015; García et al., 2018). The vouchers of species with unusual or unexpected placements in previous studies (Moore et al., 2010 and Nickrent and García, 2015) were re-examined and re-identified. The full details of vouchers used in phylogenetic inference are provided in Appendix Table S2.1.

**2.2.2 DNA Extraction. –** Genomic DNA was extracted from silica gel-dried or fresh field-collected leaf and stem samples, or from herbarium materials, using either the standard CTAB extraction protocol (Doyle and Doyle, 1987; Shutoh et al., 2016), adding a small amount of sterile sand to facilitate grinding, or the QIAGEN DNeasy kit (QIAGEN, Valencia, California, United State of America) following the manufacturer's instructions.

**2.2.3 Amplification, purification and Sequencing. –** Three plastid regions, the matK gene, the rpl32-trnL(UAG) intergenic spacer and the trnL-F region, and one nuclear marker, the internal transcribed spacer (ITS) region, were sampled using polymerase chain reaction (PCR) amplification. Some regions were difficult to amplify in some samples, resulting in missing data. However, all four markers were successfully amplified for 164 out of the 330 accessions sampled (see Appendix Table S2.1). ITS was sampled using the ITS5 and ITS4 primers of White et al. (1990), the trnL-F region was amplified using the "c" and "f" primers of Taberlet et al. (1991), the rpl32 intron using the 'trnL(UAG)' and 'rpl32-F' primers of Shaw et al. (2007), and matK using the 'matK-1RKIM-f' and 'matK-3FKIM-r' primers of Kuzmina et al. (2012).

PCR was performed in 30 µl reaction volumes, the reaction mix in each case comprising 19.3 µl distilled $H_2O$; 3 µl 10× reaction buffer; 1.2 µl magnesium chloride ($MgCl_2$) at 2.5 mM; 1.2 µl dNTP at 2.5 mM; 1 µl bovine serum albumin (BSA) at 0.05%; 1 µl of absolute dimethyl sulphoxide (DMSO); 0.9 µl at 0.3 µM concentration of primer 1 (forward) and primer 2 (reverse); 0.3 µl of normal Kapa Taq polymerase (Kapa Biosystems, Inc. Wilmington, United States) and 1.2 µl of DNA template. While maintaining the reaction volume, the amounts of DNA template, DMSO and BSA were varied between 0.5 and 1 µl according to the quality of the DNA product, and the balance reconciled with $dH_2O$. The same thermal conditions were used to amplify all regions, as follows: an initial denaturation of two minutes at 94 $^oC$; 30 cycles each comprising 94 $^oC$ for 1 min (denaturation), 48$^oC$ for 1 min (annealing) and 72 $^oC$ for 1.5 min; and a final extension of 4 min at 72 $^oC$. This protocol was amended from Nickrent and Musselman (2004) and Moore et al. (2010), the PCRs being run on an Applied Biosystems GeneAmp 2700 thermal cycler (Applied Biosystems, Foster City, CA, USA). To check the quality of amplicons, 1 µl of each sample was loaded into a well on a 1% agarose (in TBE) gel stained with ethidium bromide. The gel was then imaged under UV light. Successful amplifications were sent to Macrogen DNA sequencing facility (http://www.macrogen.com)

for DNA purification and conventional Sanger sequencing with the same primers used for amplifications.

**2.2.4 Alignment and phylogenetic analyses. –** Sequence electropherograms were assembled using the software ChromasPro version 2.1.5 (2017) and the consensus sequences then aligned using the ClustalW multiple alignment tool in MAFFT (Kuraku et al., 2013; Katoh et al., 2017). The software BioEdit v. 7.2.6 (Hall, 1999; released July 2017) was used to adjust the alignments manually. The final alignments were converted to nexus format, before being concatenated using Mesquite v3.11 (Maddison and Maddison, 2018). The final consensus sequences generated in this study were deposited in GenBank (GenBank numbers MN242082–MN242207, see Appendix Table S2.1 for details), while alignments were deposited in TreeBase (http://purl.org/phylo/treebase/phylows/study/TB2:S24838.).

Separate and concatenated parsimony heuristic and bootstrap analyses of the chloroplast [matK, rpl32-trnL(UAG) and trnL-F] and nuclear (ITS) DNA partitions were performed using PAUP* version 4.0b10 (Swofford, 2016). Each analysis employed a heuristic search procedure with 10,000 trees generated by random addition, which were subjected to tree bisection reconnection (TBR) branch swapping. Clade support was assessed using 1000 bootstrap replicates, each involving 20 replicate searches from an initial tree generated via random addition and branch-swapping via the TBR algorithm, with the number of trees saved per random addition replicate limited to 20. Bayesian inference of phylogenetic relationships was performed both for the separate matrices and for the combined matrix, using MrBayes on XSEDE version 3.2.6 x64 (Ronquist et al., 2017) as implemented in Cyber-Infrastructure for Phylogenetic Research (CIPRES) Site 2.0 (Miller et al., 2010). The best-fitting model as selected using nst=mixed command (Miller et al., 2010, Darriba et al., 2012) was implemented for each unlinked DNA dataset and for the multiple partitions. Two independent Metropolis-coupled Markov chain Monte Carlo (MCMC) runs, each consisting of one cold and three heated chains, were performed simultaneously, with samples drawn every $1000^{th}$ generation. Each run ran for $5 \times 10^7$ generations, with convergence being evaluated using the standard deviation of split frequencies. A total of 57,378 unique topologies were sampled, of which the first 25% from each run were regarded as burn-in. These were summarized as a 50% majority-rule consensus tree with branch support reflected as posterior probabilities (PP). Posterior probability values between 0.9 and 0.95 were considered weak to moderate support, while posterior probability > 0.95 was considered strong to very strong support.

Incongruence among the plastid data sets and between plastid versus ITS partitions was assessed in a pairwise manner, by comparing 50% parsimony bootstrap majority-rule consensus trees and 50% Bayesian majority-rule consensus trees for a set of taxa common to data sets. For this purpose, trees were examined visually, and conflict considered significant if both competing nodes had bootstrap support ≥ 80% and posterior probability ≥ 0.90. Hence, following Pirie (2015), taxa underpinning such incongruence were removed prior to combined analysis. The combined analysis was performed using only accessions for which data were available for both ITS and plastid partitions.

**2.2.5 Reconstruction of ancestral morphological characters.** – Forty-two morphological characters and geographical ranges were scored for all taxa included in the combined phylogenetic analyses (Fig. 2.1; Table 2.1; Appendix TableS2.2). Some of these characters had been used previously as diagnostic traits for the diagnosis of species and higher-order clades in Santalales (Hill, 1925; Pilger, 1935; Der and Nickrent, 2008; Nickrent, 2017). Character scoring was based on field notes, herbarium specimen information, online photos (http://www.phytoimages.siu.edu, https://plants.jstor.org/compilation/) and published descriptions (Hill, 1915a, 1925; Levyns, 1950; JSTOR online resources). Of the 42 morphological characters scored, 20 were binary and 22 multistate, the latter in all instances being treated as unordered (Table 2.1). The characters were optimized on the 50% majority-rule consensus tree of the Bayesian posterior trees of the combined analysis using maximum likelihood (Mk1 model) ancestral character state reconstruction as implemented in Mesquite version 3.51 (Maddison and Maddison, 2018) and the 10 most informative characters were displayed for presentation. These characters were chosen based on their diagnostic utility in previous taxonomic studies (*e.g.* Hill, 1915).

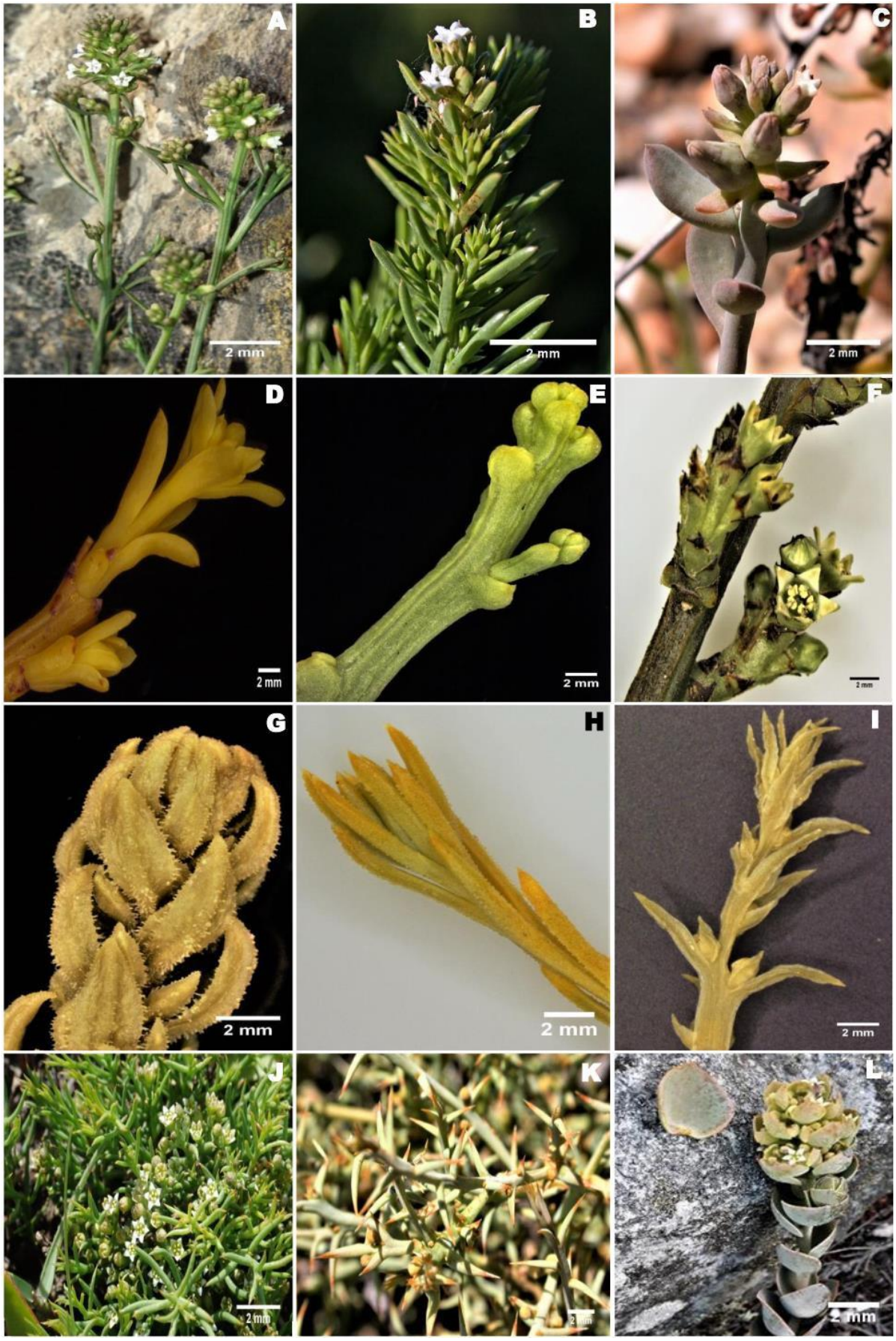



**Fig. 2.1:** Diversity in the vegetative traits of selected *Thesium* species that aid interpretation of terms used: A. leaves well-developed, sparsely distributed in *T. frisea* B. leaves well-developed,

dense or imbricate, terete to somewhat triangular in *T. imbricatum* C. stem terete, leaves succulent, moderately distributed and glaucous plant surface in *T.* sp. Schmiedel s.n. D. vegetative buds in *T. albomontanum* E. a twig with leaves modified to scales, basally subrotund, subtending a lateral shoot in *T. fragile* F. leaves imbricate, reduced to scale-like G. leaf surface hispidulous, imbricate arrangement in male *T. hirtum* H. leaf surface scabrous in *T.* sp ZM 032 I. leaf mid ribs raised, modified floral leaves (bracts) longer than flower J. leaves succulent, with spinous tips in *T. spinulosum* J. leaves and branches modified to rigid spines in *T. spinosum* K. amplexicaul leaves in *T. euphorbioides*. Photos: A and J by Odette E. Curtis, C and K by Ute Schmiedel, B by Nick Helme and the remainder by DanielA. Zhigila.

**2.2.6 Infrageneric taxonomy. –** The revised infrageneric classification presented in this study was based on the 50% majority-rule consensus tree obtained from the Bayesian analysis of the combined nuclear and plastid data sets. Since this tree included only accessions with complete sequence data, the classification of some species was, of necessity, based on their placement either in the individual gene trees (Figs 2.2–2.3, Appendix Figs. S2.1–2.4), earlier analyses (Moore et al., 2010; Nickrent and García, 2015; García et al., 2018) or a backbone constraint tree implemented in PAUP*. Morphological similarities and biogeography were also considered in the classification of such species following The World Geographical Scheme for Recording Plant Distributions (WGSRPD: Brummitt, 2001; García et al., 2018). For taxa described here as new, such as *Frisea*, or where a new status is designated, we presented the necessary information on the types, synonyms, new status/combination, etymology and list of selected voucher specimens consulted.

**Table 2.1:** Coded data matrix and their states used to identify synapomorphies in clades and subclades of *Thesium*. mm = millimeters, cm = centimeters. Missing data or where a character is not applicable, it was coded as "?". Infrageneric informative characters are indicated with an asterisk (*).

| S/N | Character | Character state | | | | |
|---|---|---|---|---|---|---|
| 1 | Growth habit* | shrub = 0 | shrublet = 1 | herb = 2 | | |
| 2 | Plant height (cm)* | < 50 | 50–100 | > 100 | | |
| 3 | Rootstock | woody = 0 | non-woody = 1 | | | |
| 4 | Aerial stem | erect = 0 | sprawling = 1 | | | |
| 5 | Stem transverse section | terete = 0 | sulcate = 1 | | | |
| 6 | Plant scabrid* | yes = 0 | no = 1 | | | |
| 7 | Branching pattern* | virgate = 0 | decumbent = 1 | intricate = 2 | divaricate = 3 | |
| 8 | Stem brittle* | yes = 0 | no = 1 | | | |
| 9 | Leaf length (mm) | < 5 | 5 – 10 | > 10 | | |
| 10 | Leafiness* | elongate, dense = 0 | elongate, sparse = 1 | scale-like = 2 | | |
| 11 | Leaf shape | linear = 0 | lanceolate = 1 | triangular = 2 | ovate = 3 | |
| 12 | Leaf attachment | decurrent = 0 | petiolate = 1 | | | |
| 13 | Leaf succulent | yes = 0 | no = 1 | | | |
| 14 | Leaf apex | acuminate = 0 | acute = 1 | obtuse = 2 | mucronate = 3 | |
| 15 | Leaf margin | entire = 0 | scabrous = 1 | serrated = 2 | | |
| 16 | Leaf margin texture | cartilaginous = 0 | not cartilaginous = 1 | | | |
| 17 | Leaf midrib | raised = 0 | not raised = 1 | | | |
| 18 | Inflorescence type* | cyme = 0 | spike = 1 | corymb = 2 | raceme = 3 | solitary = 4 |
| 19 | Flower shape* | patelliform = 0 | hypocrateriform = 1 | urceolate = 2 | | |
| 20 | Peduncle | absent = 0 | present = 1 | | | |
| 21 | Floral bract aspect* | longer to equalling the flower = 0 | shorter to equalling the flower = 1 | | | |
| 22 | Flower bract shape | Leaf-like = 0 | scale-like = 1 | | | |
| 23 | Bracteole | present = 0 | absent = 1 | | | |
| 24 | Flower merosity* | mostly 4-merous = 0 | mostly 5-merous = 1 | | | |

| | | | | | |
|---|---|---|---|---|---|
| 25 | Hypanthium tube aspect | conspicuous = 0 | inconspicuous = 1 | | |
| 26 | Anther* | above stigma = 0 | below stigma = 1 | below or in line with stigma = 2 | dioecious = 3 |
| 27 | Perianth lobe apical trichome* | absent = 0 | present = 1 | | |
| 28 | Perianth lobe shape | lanceolate = 0 | triangular = 1 | | |
| 29 | Perianth lobe tip | distinctly uncinate = 0 | not or indistinctly uncinate = 1 | | |
| 30 | Perianth lobulate | yes = 0 | no = 1 | | |
| 31 | Perianth lobe margin | entire = 0 | ciliated = 1 | undulate = 2 | |
| 32 | Perianth lobe inside colour | white = 0 | green = 1 | | |
| 33 | Perianth lobe outside colour | green = 0 | white = 1 | black = 2 | grey = 3 |
| 34 | Fruit surface | glabrous = 0 | reticulate = 1 | | |
| 35 | Fruit shape | ovoid = 0 | elliptic = 1 | truncated= 2 | |
| 36 | Fruit elaiosome | absent = 0 | present = 1 | | |
| 37 | Fruit rib | 10-ribbed = 0 | 5-ribbed = 1 | no ribs = 2 | |
| 38 | Fruit colour | green = 0 | white = 1 | | |
| 39 | Fruit length (mm) | mm | | | |
| 40 | Fruit width (mm) | mm | | | |
| 41 | Length of persistent perianth segment | shorter than fruit = 0 | longer than fruit = 1 | equal to fruit = 2 | |
| 42 | Geographical range* | South Africa = 0<br>South America = 3<br>Subtropical Africa = 6 | Tropical Africa = 1<br>Canary Island = 4 | Eastern Asia = 2<br>Europe/Western Asia = 5 | |

## 2.3 RESULTS

**2.3.1 Properties of the sequence data –** The properties of each data set are indicated in Table 2.2. Of the 234 ITS, 223 trnL-F and 122 matK DNA sequences used in the phylogenetic analyses, 126, 117 and 114, respectively, were newly generated for this study. Although ITS has a much higher percentage of potentially parsimony-informative sites, the total number of parsimony-informative sites is greater for the plastid loci on account of the larger number of plastid sequences used. Differences in the number and phylogenetic distribution of informative characters in the plastid and ITS DNA regions mirror the higher phylogenetic signal in the ITS tree obtained.

**Table 2.2** Properties of the six data sets used for phylogenetic analyses.

| Locus | No. of accessions | No. of species | Best-fit model | Sequence length | Parsimony-informative characters |
|---|---|---|---|---|---|
| ITS | 234 | 155 | GTR+I+G | 851 | 458 (54%) |
| matK | 165 | 119 | GTR+G | 961 | 242 (25%) |
| rpl32_trnL | 122 | 110 | TPMluf+I+G | 776 | 253 (33%) |
| trnL-F | 223 | 153 | TIM1+G | 1266 | 485 (38%) |
| Combined plastid | 254 | 163 | T92+G | 2928 | 747 (26%) |
| Plastid +nuclear | 164 | 110 | GTR+I+G | 4242 | 1450%) |

**2.3.2 Separate analyses and assessment of incongruence –** Comparison of the 50% majority-rule consensus trees based on the Bayesian posterior probability tree sets generated for the individual plastid markers reveal no reciprocally supported incongruence between any pair of loci (Appendix Figs S2.2 – 2.4). The five major clades (nodes 1–5) are consistently well-supported, but the internal nodes show variable support. In the absence of reciprocally-supported incongruence among the individual plastid loci, the data sets were analysed in combination, yielding a tree which shows generally improved nodal supports (Fig. 2.2B).

Comparison of the topologies derived from the combined plastid and ITS data sets revealed substantial agreement in the delimitation of major clades within *Thesium* (Fig. 2.2A–B). Overall, the five major clades (nodes 1 to 5) are consistently well-supported in both plastid and ITS trees, though there were instances of reciprocally-supported incongruence at this level: (i) where ITS placed *T. minus* within clade 1 as sister to *T. microcarpum* (BS = 100%, PP = 0.99), the plastid data resolved it within subclade C of clade 5 (BS = 98%, PP = 0.92) of *T. ericaefolium* and allies; (ii) where ITS recovered one

accession of *T. corymbuligerum* (H1604) in clade 4, sister to *T. acutissimum* (BS = 100%, PP = 1), the plastid data set placed it in subclade C of clade 5 (BS = 96%, PP = 0.90); (iii) where ITS resolved *T. whitehillensis* as sister to a clade comprising clades 3, 4 and 5 (BS = 97%, PP = 0.99), the plastid data resolved it as sister to clade 3 (BS = 100%, PP = 1). Furthermore, within clades 1 to 4, the relationships suggested by ITS and the plastid data are also broadly congruent, though the placements of two species are discordant with reciprocal-support: (i) where ITS places *T. squarrosum* as sister to *T. scandens* (BS = 100%, PP = 1), the plastid data resolve it as sister to *T. galioides* (BS = 98%, PP = 1); and (ii) where ITS resolves *T. angulosum* as sister to *T. transvaalense* and allies, the plastid data resolve this species in a polytomy comprising *T. costatum* and allies (BS = 96%, PP = 0.96). Although the monophyly of clade 5 is strongly supported by both the ITS (BS = 100%, PP = 0.99) and plastid (BS = 100%, PP = 0.96) data sets, both leave some internal nodes unresolved and, perhaps more importantly, these data sets are incongruent with respect to the placement of several taxa. The presence of various instances of supported incongruence between the plastid and ITS data trees necessitated the exclusion of incongruent taxa prior to combined analysis. Accordingly, 18 (11%) accessions representing 13 species, mostly belonging to clade 5 (Fig. 2.2), were omitted from the combined analysis, this bringing the two data sets into agreement.

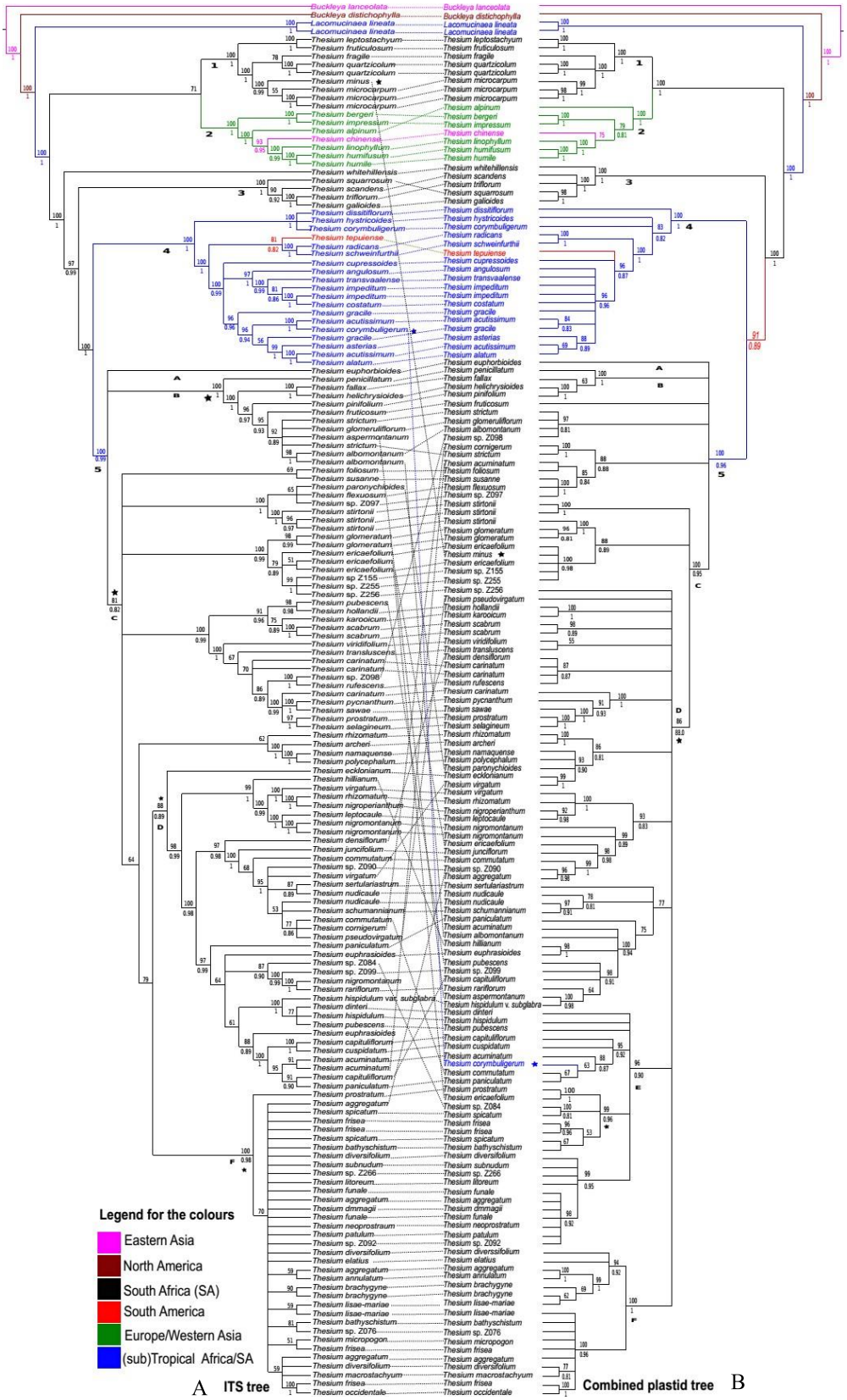



**Fig. 2.2:** The 50% majority-rule phylogenetic trees obtained from the Bayesian analyses A nuclear gene (ITS) and B concatenated cpDNA matrix (matK, rpl32-trnL and trnL-

trnF). Numbers above and below each branch represent bootstrap support values (> 60%) and posterior probabilities (> 0.8), respectively. Coloured leaves and taxa names show geographical range estimates of species. Numbers 1–5 and letters A–E indicate nodes discussed in the text. Black stars denote taxa with reciprocal conflicts in both gene trees. Dotted lines at terminal tips indicate taxon matches between the ITS and the plastid gene trees.

**2.3.3 Combined plastid and nuclear analyses. –** The tree resolved by analyses of the four-marker concatenated dataset is broadly congruent with those resolved by separate analyses of the ITS and plastid data with the support on most nodes being much stronger (Fig. 2.3). Relative to the outgroups (*Buckleya* and *Lacomucinaea*) included in this study, the monophyly of the genus *Thesium* is supported (BS = 100%, PP = 1). Within *Thesium*, the five major clades identified by the separate ITS and plastid partitions are retrieved with strong support, with the relationships between these clades also being unambiguous and strongly-supported. Clade 1 (BS = 100%, PP = 1), comprising exclusively GCFR- endemic species, and clade 2 (BS = 100%, PP= 1), comprising the Eurasian taxa, are strongly supported as sister lineages (BS = 100%, PP = 1), the pair being resolved as sister to a well-supported (BS = 100%, PP = 1) clade comprising clades 3, 4 and 5. Within the latter, clade 3 (BS = 97%, PP = 0.99) comprises species distributed from the Succulent Karoo to the eastern parts of the GCFR, clade 4 (BS = 100%, PP =1) comprises the tropical African and South American species, and clade 5 is strongly Cape-centred, being composed almost entirely of Succulent Karoo, Renosterveld and Fynbos species. Within clade 5, six major lineages are resolved (Fig. 2.3), namely: (a) *T. euphorbioides*; (b) a strongly-supported clade comprising *T. penicillatum* and allies (BS = 100%, PP = 1); (c) a weakly-supported clade (BS = 76%, PP < 0.90) comprising three more strongly- supported subclades: *T. archeri* and allies (BS = 87%, PP = 0.90), *T. nigromontanum* and allies (BS = 100%, PP = 1) and *T. ericaefolium* and allies (BS = 91%, PP = 0.96); (d) a strongly-supported clade comprising *T. euphrasioides* and allies (BS = 100%, PP = 1); (e) a moderately well-supported clade (BS = 90%, PP = 0.91) comprising *T. ecklonianum* and a well-supported clade of leafy species (BS = 100%, PP = 1); and (f) a strongly- supported clade comprising *T. frisea* and allies (BS = 100%, PP = 1).


**Fig. 2.3:** The 50% majority-rule phylogenetic tree obtained from the Bayesian analyses of the concatenated molecular datasets (ITS + matK+ rpl32-trnL + trnL-F). The clades

representing subgenera and sections as well as outgroups are indicated by vertical lines and relevant names. Coloured lines and branch tips show geographical range estimates of species. Numbers above branches indicate bootstrap percentages > 60% and below branches indicate posterior probability values > 0.8. Numbers 1–5 and letters a–f indicate nodes discussed in the text.

**2.3.4 Morphological characters.** –Ancestral character state reconstructions identified diagnostic morphological synapomorphies or symplesiomorphies for all clades recognized at subgeneric level, although these traits were in some instances homoplasious (Fig. 2.5A–J). For *T. fragile* and allies (clade 1), putative synapomorphies include the possession of brittle stems , not only when dry, but also in the fresh state (Appendix Fig. S2.4A). In addition, a dioecious breeding system (Fig. 2.5J), predominantly four-merous flowers (five-merous flowers rarely occur in *T. fragile*), a four-merous androecium and perianth lobes with green inner surfaces (Fig. 2.5H) are synapomorphic for this clade. Truncate fruit with a swollen, white elaiosome and persistent pinkish to yellowish perianth segments is autapomorphic in *T. fragile* (Fig. 2.4P, Appendix Fig. S2.4, Table 2.1). The ancestral spicate inflorescence observed in clade 1 (*e.g.* in Fig. 2.4C, D and H) has elsewhere evolved to produce the diversity of inflorescence morphologies seen in *Thesium* (Fig. 2.5F).

For *T. alpinum* and allies (clade 2), diagnostic synapomorphies include racemose inflorescences (Fig. 2.5F) and inclusion of the stamens below or at the same level as the stigma (Fig. 2.5J). Where the first of these characters has arisen several times independently in *Thesium*, the latter occurs elsewhere only in *T. tepuiense*. Also, the presence of hair-like structures covering the entire plant surface and giving it a silvery glaucous appearance may be considered apomorphic for *T. mauritanicum* (Appendix Table S2.2). For clade 3, synapomorphies include divaricate branching pattern (Fig. 2.5B), which is unique to this clade, and the sparse occurrence of elongate (i.e. linear to lanceolate; not scale-like) leaves, which has, however, also evolved twice independently in clade 5. For example, the leaves are reduced to scale-like, sparse in *T. nigromontanum* and allies or elongate, imbricate in *T. flexuosum*. Leaf characters thus present considerable heterogeneity both within and among subgenera (Fig. 2.5D). In the subtropical-tropical clade 4, *T. gnidiaceum* and allies are characterised by an intricate branching pattern (Fig. 2.5B), scale-like leaves (Fig. 2.5D) and floral bracts which are consistently shorter than the flower (Fig. 2.5E). Although these traits have arisen several times independently in other clades, they are potential synapomorphies for this subclade.

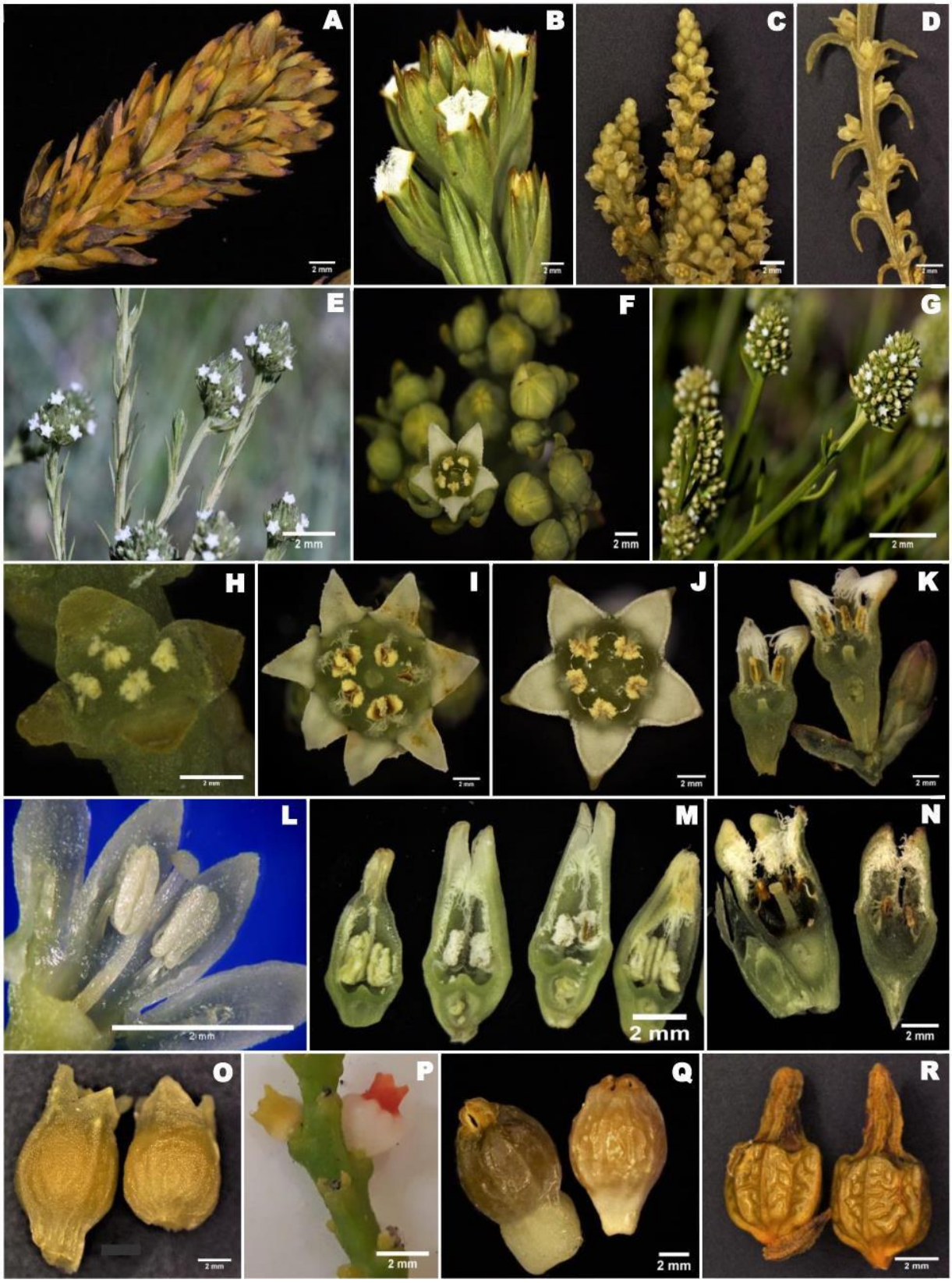
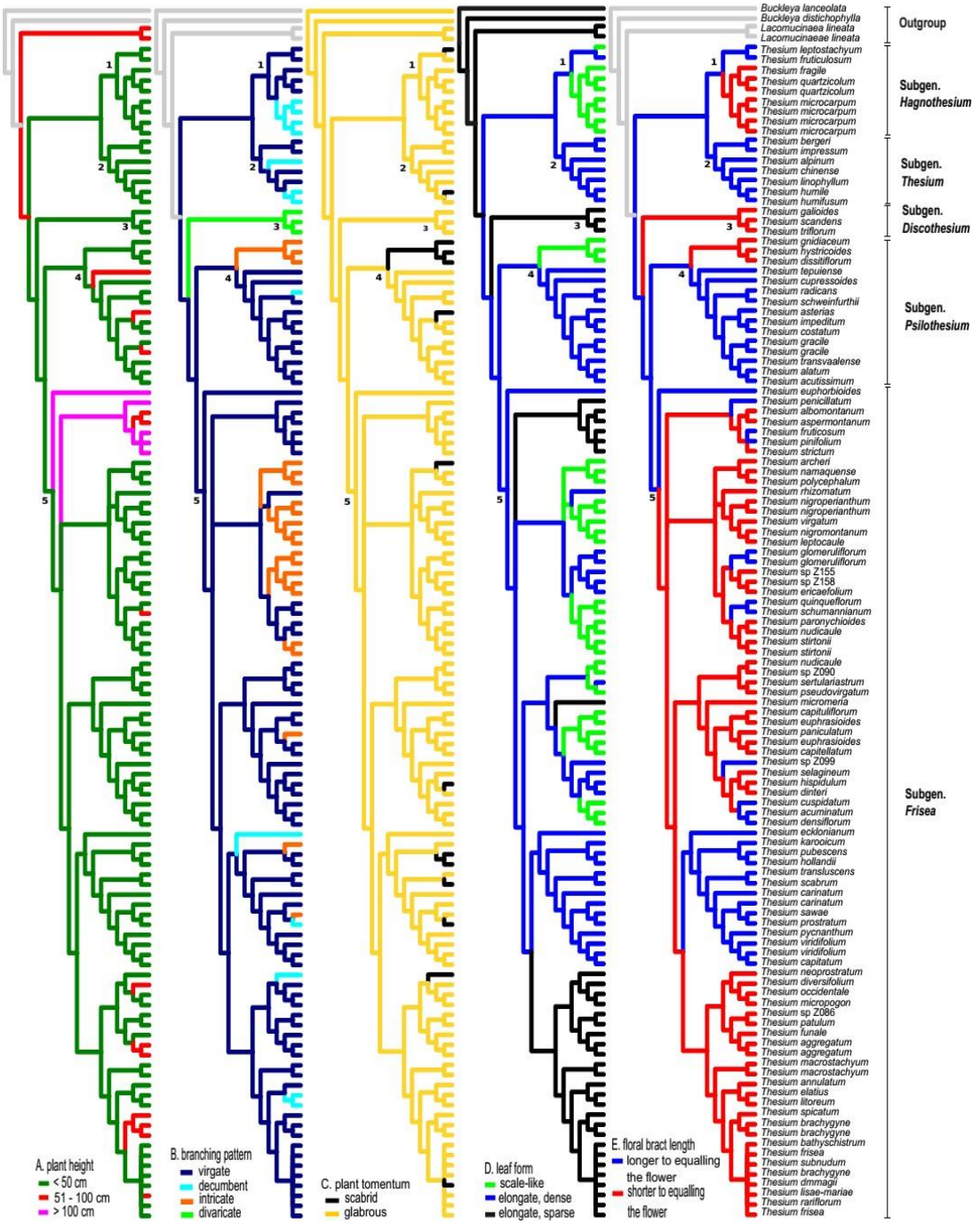

A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
2 mm

**Fig. 2.4:** Floral and fruit diversity in *Thesium*: inflorescence arrangements A. elongated spike in *T. spicatum* B. terminal compact spikes, bract longer or equaling flower length, perianth lobe with apical trichome tuft in *T. carinatum* C. and D. axillary spike in *T. microcarpum* and *T. minus,* respectively E. terminal conical spikes in *T. dmmagiae* F. terminal compact corymbs in *T. strictum* G. terminal globose spikes in *T. frisea*; flower merosity H. 4-merous; 4-stamen flower and green perianth lobe inside colour in *T. fragile* I. a teratological 7-merous flower in *T. stirtonii* J. 5-merous flower; perianth lobe apical trichome absent; with a papillose lobe margins in *T. nigroperianthum*; flower longitudinal sections showing anther/stigma relationship K. anther above stigma; style short; placental column twisted in *T. dmmagiae* L. anther below stigmas; style long in *T. impressum* M. anther above stigmas; style sessile to subsessile; placental column twisted in *T. neoprostratum* N. anther in line with stigmas; style long in *T. aggregatum*; fruit characters O. 5-ribbed, inconspicuous reticulation on the fruit surface of *T. quartzicolum* P. white fruit capped with yellowish and pinkish persistent perianth segment in *T. fragile* Q. interspecific variations of truncated and tapering elaiosome in *T. scabrum* R. 10- ribbed, conspicuous reticulation and long persistent perianth segment in *T. zeyheri*. Photos: E and G by Odette E. Curtis, L by Daniel L. Nickrent from Castroviejo & Nissa 15890SC voucher, the remainder by Daniel A. Zhigila.

Clade 5 possesses floral bract shorter or equalling the flower as a potential synapomorphy within which multiple reversals to longer or equalling the flower in other lineages (Fig. 2.5E). Within clade 5, *Thesium euphorbioides*, the monotypic lineage (*Aetheothesium*), is unique and distinctive in having ovate, amplexicaulous leaves with a cordate base and a mucronate tip (Fig. 2.1L; Appendix Fig. S2.4B), which was considered autopomorphic character to this species. The placement of *T. ecklonianum* as sister to the rest of subclade 5E (BS = 90%, PP = 0.91) is supported by its greyish overall plant colour, succulent leaves, terete stem and scars of floral abortion, all characters assumed to be apomorphic for the taxon (Appendix Table S2.2). Most species in clade 1, clade 2 (except in *T. bergeri* and allies), clade 3, clade 4 (except in *T. costatum* and allies) and clade 5 subclades A–C have a patelliform flower shape (Fig. 2.5G). Interestingly, this patelliform flower mostly corresponds to the absence of perianth lobe apical trichomes (Figs 2.4F, I, J and 2.5E). Then, hypocrateriform and urceolate flowers corroborate well with the presence of tuft of perianth lobe apical trichomes (Figs 2.4K, D and 2.5H). Species with scabrid to hispidulous surfaces as putative homoplasy are found sparingly across clades and subclades (Fig. 2.5C) *e.g. T. hirtum, T. pubescens, T. scabrum* and *T. humile*.


Buckleya lanceolata
Buckleya distichophylla
Lacomucinaea lineata
Lacomucinaeae lineata
Outgroup
Thesium leptostachyum
Thesium fruticulosum
Thesium fragile
Thesium quartzicolum
Thesium quartzicolum
Thesium microcarpum
Thesium microcarpum
Thesium microcarpum
Thesium microcarpum
Subgen. Hagnothesium
Thesium bergeri
Thesium impressum
Thesium alpinum
Thesium chinense
Thesium linophyllum
Thesium humile
Thesium humifusum
Thesium galioides
Thesium scandens
Thesium triflorum
Subgen. Thesium
Subgen. Discothesium
Thesium gnidiaceum
Thesium hystricoides
Thesium dissitiflorum
Thesium tenuense
Thesium cupressoides
Thesium radicans
Thesium schweinfurthii
Thesium asterias
Thesium impeditum
Thesium costatum
Thesium gracile
Thesium gracile
Thesium transvaalense
Thesium alatum
Thesium acutissimum
Subgen. Psilothesium
Thesium euphorbioides
Thesium penicillatum
Thesium albomontanum
Thesium aspermontanum
Thesium fruticosum
Thesium pinifolium
Thesium strictum
Thesium archeri
Thesium namaquense
Thesium polycephalum
Thesium rhizomatum
Thesium nigroperianthum
Thesium nigroperianthum
Thesium virgatum
Thesium nigromontanum
Thesium leptocaule
Thesium glomeruliflorum
Thesium glomeruliflorum
Thesium sp Z155
Thesium sp Z158
Thesium ericaefolium
Thesium quinqueflorum
Thesium schumannianum
Thesium paronychioides
Thesium nudicaule
Thesium stirtonii
Thesium stirtonii
Thesium nudicaule
Thesium sp Z090
Thesium sertulariastrum
Thesium pseudovirgatum
Thesium micromeria
Thesium capituliflorum
Thesium euphrasioides
Thesium paniculatum
Thesium euphrasioides
Thesium capitellatum
Thesium sp Z099
Thesium selagineum
Thesium hispidulum
Thesium dinteri
Thesium cuspidatum
Thesium acuminatum
Thesium densiflorum
Thesium ecklonianum
Thesium karooicum
Thesium pubescens
Thesium hollandii
Thesium transluscens
Thesium scabrum
Thesium carinatum
Thesium carinatum
Thesium sawae
Thesium prostratum
Thesium pycnanthum
Thesium viridifolium
Thesium viridifolium
Thesium capitatum
Thesium neoprostratum
Thesium diversifolium
Thesium occidentale
Thesium micropogon
Thesium sp Z086
Thesium patulum
Thesium funale
Thesium aggregatum
Thesium aggregatum
Thesium macrostachyum
Thesium macrostachyum
Thesium annulatum
Thesium elatius
Thesium litoreum
Thesium spicatum
Thesium brachygyne
Thesium brachygyne
Thesium bathyschistrum
Thesium frisea
Thesium subnudum
Thesium brachygyne
Thesium dmmagii
Thesium lisae-mariae
Thesium rariflorum
Thesium frisea
Subgen. Frisea
A. plant height
< 50 cm
51 - 100 cm
> 100 cm
B. branching pattern
virgate
decumbent
intricate
divaricate
C. plant tomentum
scabrid
glabrous
D. leaf form
scale-like
elongate, dense
elongate, sparse
E. floral bract length
longer to equalling the flower
shorter to equalling the flower

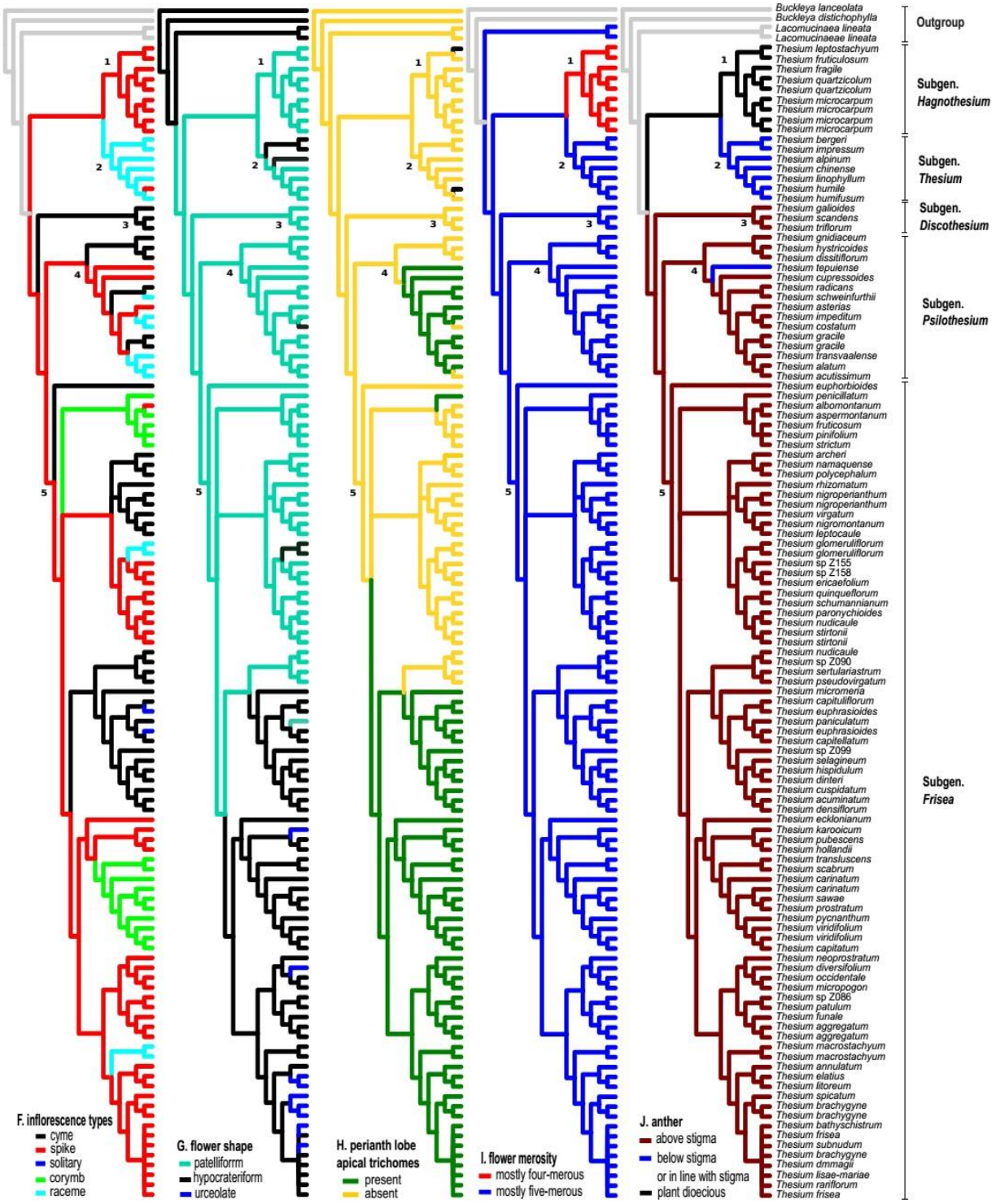



**Fig. 2.5 (A – J):** Optimized morphological traits on the combined Bayesian phylogenetic tree to estimate ancestral character evolution of ten representative traits in *Thesium.* The legend explains the colours used to depict the character evolutionary patterns. Grey colour of the outgroups indicates characters not studied. Numbers 1–5 indicate major clades (subgenera) discussed in the text.

## 2.4 DISCUSSION

This study is consistent with previous works (Moore et al., 2010; Nickrent and García, 2015) in supporting the inclusion of *Austroamericium*, *Chrysothesium*, *Kunkeliella* and *Thesidium* in *Thesium*. The expanded sampling of taxa and loci, however, gives both a more complete picture of species relationships and considerably improved cladesupport, particularly within the hitherto weakly-resolved Cape clade (Fig. 2.3). Given that two independently-assorting DNA partitions (ITS and plastid) provide robust support for five major clades within *Thesium*, and that some of these clades are further corroborated by distinct geographical associations and morphological characters, this study provides a suitable foundation for an infrageneric classification scheme (Table 2.3). Building on the classification proposed by Moore et al. (2010), we recognize the five strongly supported clades as subgenera (Fig. 2.3), namely: *Thesium* subgenus *Hagnothesium* A.DC. (clade 1), *Thesium* subgenus *Thesium* L. (clade 2), *Thesium* subgenus *Discothesium* A.DC. (clade 3), *Thesium* subgenus *Psilothesium* A.DC. (clade 4) and *Thesium* subgenus *Frisea* (Reichenb.) Hendr. (clade 5).

The Cape-endemic subgenus *Hagnothesium* is sister to the mostly-Eurasian subgenus *Thesium* (BS = 100%, PP = 1) with which it shares glabrous perianth lobe tips (Fig. 2.5H), a predominantly short (< 50 cm tall) stature (Fig. 2.5I; Hendrych, 1972) and generally patelliform perianth segments. The two subgenera are, however, distinguishable by differences in stamen number: where subgenus *Hagnothesium* typically has four stamens per flower (Fig. 2.4H), subgenus *Thesium* typically has five (Fig. 2.4J), although flowers with four, six or even seven stamens do occur (Fig. 2.4I) as teratological variants. In addition, they differ in terms of breeding system, subgenus *Hagnothesium* being dioecious and subgenus *Thesium* hermaphroditic (Der and Nickrent, 2008; Forest and Manning, 2013). Within subgenus *Hagnothesium*, the type species (*T. fragile*) and allies are easily distinguished by their brittle stems, truncate fruits and persistent, green perianth lobe segments that turn first yellow and then orange at maturity (Fig. 2.4P). The node subtending *T. fruticulosum* and allies on the other hand, is characterized by sexual dimorphism (Hill, 1925; Forest and Manning, 2013), with the bracts and bracteoles being much longer (about three times) than the flowers in female plants and highly reduced in male plants (Fig. 2.5I; Zhigila et al., 2019b).

The name *Thesium* is adopted here for subgenus *Thesium* against the previous *Euthesium*, following Article 22.1 of the International Code of Botanical Nomenclature

(Shenzeng Code; Turland et al., 2018): “The name of any subdivision of a genus that includes the type of the adopted, legitimate name of the genus to which it is assigned is to repeat that generic name unaltered as its epithet, not followed by an author citation”. Since (i) Hitchcock (1929) explicitly designated *T. alpinum* as the lectotype species for *Thesium*, (ii) the etymology of species names in the clade have not revealed any tangible morphological descriptions that best fit any of the clades to *Thesium*, and (iii) *T. alpinum* is nested within the clade corresponding to section *Euthesium*, we favour the name *Thesium* for this clade.

Although incomplete marker sampling resulted in neither *T. mauritanicum* nor section *Kunkeliella* being represented in our combined-four-marker phylogeny (Fig. 2.3), the results of earlier analyses (Forest and Manning, 2013; Nickrent and García, 2015; García et al., 2018) and our ITS tree (Appendix Fig. S2.1, BS = 100%, PP = 1) identify these lineages as being closely allied to, though not necessarily included within the subgenus *Thesium*. Moreover, although *Kunkeliella* is distinguished “by its isopolar pollen and drupaceous fruit” (Stearn 1972) and discrete geographical distribution (Canary Island endemics), it shares characters such as patelliform flowers, perianth lobe apices without trichomes, generally five-merous flowers and adnate leaves with members of subgenus *Thesium*. For these reasons we include this lineage within subgenus *Thesium*. The inclusion of *Kunkeliella* in the subgenus *Thesium* necessitates the inclusion in *Thesium* of Hendrych’s series *Mauritanica*, established in 1972 to accommodate the North African *T. mauritanicum* and *T. erythronicum*. Series *Mauritanica* (Bobrov, 1936) is distinct from other members of *Thesium* by its recurved leaves and silvery glaucous appearance (Hendrych, 1972), the latter being attributable to the presence of trichomes all over the plant’s surface (Peltier, 2015). In members of the subgenus *Thesium*, style elongation ensures that the stigma is held above the anthers (Hill, 1925). Based on our reconstructions (Fig. 2.5J), this trait is homoplaseous for species in these clades, while stigma held below anthers is a synapomorphy for the remaining subgenera (sister to *Thesium* clades). Only a single species (*T. tepuiense*) has lost this trait.

The monophyly of *Thesium* subgenus *Discothesium* (clade 3; BS = 97%, PP = 1) is supported by its member species being with divaricate branching pattern (Fig. 2.5B). Based on the ancestral character reconstruction, the branching pattern is considered a synapomorphy for this clade. In addition, leaves being linear to linear-lanceolate and the disc-like perianth lobes unite species in this clade. De Candolle (1857b) established a section for this clade based on the well-marked perianth disc of the flower (Hill, 1915a). This sectional recognition was reversed by Hill on the ground that it is insufficient to warrant the rank. In this study, the divaricate branching pattern, lanceolate leaf shape and well-marked perianth disc supports the monophyly of this clade. The subgenus *Discothesium* comprises species distributed from the summer rainfall areas of the Western Cape, toward the Succulent Karoo and to the eastern parts

of the GCFR.

Although subgenus *Psilothesium* contains highly disjunct species from (sub)tropical Africa and tropical South America, its monophyly is well-supported (BS = 100%, PP = 1). The South American species (here represented by *T. tepuiense*) were previously treated as a separate genus (*Austroamericium*; Hendrych, 1972) or as a separate section (*Chrysothesium*) of *Thesium* (De Candolle, 1857b; Pilger, 1935), but their placement within a clade of (sub)tropical African species (García et al., 2018 and Figs 2.2 and 2.3) necessitates their inclusion in subgenus *Psilothesium*. Most likely, the disjunct distribution of these species is a product of anthropogenically-mediated long-distance dispersal Musselman and Haynes (1996), not vicariance (Hendrych, 1972; Moore et al., 2010; Nickrent and García, 2015). Within subgenus *Frisea*, there is little correspondence between the major clades resolved by the combined data analysis presented here (i.e. clades A–F, Fig. 2.3) and the classification schemes suggested by either Hill (1915a; 1925), Bobrov (1936) or Hendrych (1972). Thus, any future sectional treatment of this subgenus will most certainly require major changes. In addition, beyond the core set of species retained in the combined analysis, subgenus *Frisea* shows high levels of incongruence, with the placement of several species in ITS and plastid trees being contradictory, and some conspecific accessions being widely separated (Fig. 2.2). Given the presence of several polytomies near the base of clade 5, and the rapid diversification that these imply, we suspect that this incongruence is largely a consequence of incomplete lineage sorting. However, given that the ranges of many species within subgenus *Frisea* overlap, we cannot exclude the role for hybrid-mediated horizontal gene transfer (Potts et al., 2018). Unfortunately, our data lack the resolution to distinguish between these alternative explanations, which we anticipate will require the application of high-throughput, next-generation sequencing technologies.

In subgenus *Frisea*, the combined analysis with incongruent taxa omitted resolved some well-supported clades, which are morphologically distinct. Some of these clades correspond roughly, either in terms of their species membership or their morphological characteristics, to supraspecific taxa previously delimited by Hill (1915), and the idea of splitting subgenus *Frisea* into a series of sections is consequently tempting. However, incongruence in the placement of *Imberbia* and *Barbata* (sensu Hill, 1915) species within the subgenus means that a formal sectional classification is probably premature. We therefore suggest, within a phylogenetic comparative context, assess cases of introgressive hybridization for the excluded accession in future studies. In the meantime, however, we recognize a set of informal species groups, which are morphologically-distinct and correspond broadly to the clades and or lineage (Fig. 2.3, clade 5a-f) defined by the combined analysis. These are: A) *Aetheothesium* (comprising only *T. euphorbioides*); B) the *Penicillata* group; C) the *Imberbia* group; D) the *Barbata* group; E) the

Leafy group; and F) the *Frisea* group.

The isolated position of the monotypic lineage *Aetheothesium* (*T. euphorbioides*; Figs 2.2 and 2.3), which reflects the findings of Moore et al. (2010) and Nickrent and García (2015), is unsurprising given the distinct morphology of this species (Fig. 2.1L). Although several characters, including stem-adpressed, glaucous leaves, pentamerous flowers, conspicuous external glands between the perianth lobes, anthers held above the stigmas (Fig. 2.5J) and nut-like fruits having short pedicels modified to form elaiosomes (Appendix Table S2.2), unite *T. euphorbioides* with the rest of clade 5, this species possesses several traits that make it quite distinct. These include its broadly-ovate or suborbicular, coriaceous, imbricately- arranged leaves, with their cordate bases that encircle their subtending branches (amplexicaul) and their mucronate apices (Fig. 2.1L). Since the placement of *T. euphorbioides* in clade 5 is well-supported by both the plastid and ITS data (Fig. 2.2A, B), however, we include this species, and the Candollean section (i.e. *Ætheothesium* = *Aetheothesium* Hill, 1915) in subgenus *Frisea*.

Hill (1915) described section *Penicillata* as monotypic with only *T. penicillatum,* which is characterized by perianth lobes possessing a tuft of apical trichomes, anthers with attachment hairs and is endemic to South Africa. Our analyses, however, identify *T. penicillatum* as a member of a well-supported clade (subclade B, BS = 100%, PP = 1) of ten closely related species (BS = 98%, PP = 1) to subclade comprising solely of the GCFR taxa. We therefore expand the *Penicillata* group to accommodate this entire clade. Potential synapomorphies of this clade includes large plant size (100–250 cm tall; Fig. 2.5A) and glabrous to minutely papillose perianth lobe margins (Fig. 2.4J, Appendix Table S2.2). Other morphological traits of this clade include patelliform flowers (Fig. 2.5G), the presence of conspicuous external glands between the perianth lobes, and the presence of a ring of hairs on the back of the anther (Appendix Table S2.2). Since *T. penicillatum* is exceptional in lacking the anther hair ring, Hill's (1915) characterization of section *Penicillata* as having "anthers free from attachment hairs" is clearly at odds with our characterization of the *Penicillata* group as defined here.

**Table 2.3:** Updated historical infrageneric development in *Thesium*. Modified from Moore et al. (2010) to reflect treatment from this study. Sect. = section, gen. = genus, subgen. = subgenus. Hill's study did not include sections *Chrysothesium* and *Psilothesium* (N/A).

| Sonder (1857) | De Candolle (1857b) | Hill (1915, 1925) | Pilger (1935) | Hendrych (1963, 1972) | Zhigila et al. (2020) |
|---|---|---|---|---|---|
| | Sect. *Frisea* | Sect. *Annulata*<br>Sect. *Barbata*<br>Sect. *Penicillata* | Sect. *Frisea* | Subgen. *Frisea* | Subgen. *Frisea* |
| | Sect. *Aetheothesium* | Subsect. *Subglabra* | | | |
| | Sect. *Euthesium* (*Thesium*) | Sect. *Imberbia*<br>Subsect. *Fimbriata* | Sect. *Euthesium* (*Thesium*) | Subgen. *Thesium* (*Thesium*) | Subgen. *Thesium* |
| | Sect. *Chrysothesium* | N/A | | Sect. *Chrysothesium* | |
| | Sect. *Discothesium* | Subsect. *Subglabra* | | Sect. *Imberbia* | Subgen. *Discothesium* |
| | Sect. *Psilothesium* | N/A | Sect. *Psilothesium* | Gen. *Austroamericium* | Subgen. *Psilothesium* |
| Gen. *Thesidium* | Sect. *Hagnothesium* | Gen. *Thesidium* | Gen. *Thesidium* | Gen. *Thesidium* | Subgen. *Hagnothesium* |

The remaining subclades (C–F) within clade 5 are all broadly distinguishable by one or two synapomorphic traits, as follows: although clade C lacks clear synapomorphies, most of its members possess an intricate branching pattern (Fig. 2.1B); subclade D is defined by cymose inflorescences in its component species (Fig. 2.1F); subclade E members are broadly recognizable by the floral bracts equalling to exceeding the flowers in length, with corymbose inflorescences defining a core subclade; and clade F is characterized by its possession of sparsely-distributed elongate leaves (Fig. 2.5D). In addition, a more inclusive clade, comprising subclades D–F is characterized by mainly hypocrateriform flowers, with independent reversal to an urceolate shape, presence of dense apical trichomes on perianth lobes, except in *T. pseudovirgatum* and allies (Fig 2.5H) and attachment of the anthers to the perianth tubes by a tuft of hairs in the form of a ring downwardly directed and inserted at the base of the perianth tubes, a character Hill (1915) described as unique to section *Annulata* (Fig. 2.4N– R; Appendix Table S2.2). Albeit, the morphology-based sectional classification scheme of Hill (1915, 1925) is clearly untenable owing to the non-monophyly of sections as revealed by molecular data in conjunction with ancestral character reconstructions enumerated above. For example, species previously included in section *Imberbia*, subsections *Fimbriata* and *Subglabra* (Hill, 1915), section *Euthesium* (De Candolle, 1857b; Pilger, 1935) and subgenus *Thesium* (sensu Hendrych, 1972) were recovered here as a clade.

## 2.5 CONCLUSIONS

We present a comprehensive, phylogenetically-based infrageneric classification of *Thesium* based on a combination of geographical range, molecular and morphological evidence. Five subgenera are recognised, which are convincingly supported not only by a combined molecular analysis, but also by separate analyses of plastid and ITS sequences. To a large extent, these subgenera are morphologically diagnosable. In addition, we provide unequivocal support for the inclusion of the segregate genera *Austroamericium, Chrysothesium, Kunkeliella* and *Thesidium* in *Thesium.* The phylogeny reflects strong biogeographic pattern with all subgenera, except *Thesium* and *Psilothesium*, being centred in the GCFR of South Africa (Fig. 2.3). This is consistent with the propositions of Hendrych (1972) and Moore et al. (2010) that the genus originated in South Africa. In the sections that follow, we provide (i) a key to the subgenera, (ii) a brief morphological description of each subgenus, along with a description of its distribution ranges and ecology; and (iii) a list of the species assigned to each subgenus.

## 2.6 TAXONOMIC IMPLICATIONS

### 2.6.1 Key to the subgenera of *Thesium* (Fig. 2.3; Table 2.3)

1. Plants dioecious, flower mostly 4-merous, rarely 5-merous, perianth inside and outside colour yellowish green to green, mature fruit green or white, GCFR endemic… .....**2.6.2.1. *T.*** subgenus ***Hagnothesium***

1. Plants hermaphroditic, flower mostly 5-merous, perianth inside colour white, outside colour green or black, mature fruit green, rarely white, wide spread….....2

2. Fruits drupes or nutlets, fleshy or dry, mostly Eurasian..... **2.6.2.2**. ***T.*** subgenus ***Thesium***

2. Fruits nut-like and dry, not Eurasian…….....3

3. Annual herbs or suffrutices, leaves subterete or defined into adaxial and abaxial surfaces, bracts longer than flower, rarely equal or shorter, subtropical or tropical African/South American …….....**2.6.2.4. *T.*** subgenus ***Psilothesium***

3. Perennial shrubs, shrublets or undershrubs, leaves terete or somewhat triangular, otherwise amplexicaul or scale-like, bracts shorter to longer than flower, not tropical…….4

4. Plants branching pattern polymorphic, but not divaricate, leaves polymorphic, flower shape polymorphic, South African. ...…...…… **2.6.2.5. *T.*** subgenus ***Frisea***

4. Plants branching pattern divaricate, rarely intricate, leaves linear or modified to spines, flower shape patelliform, subtropical ……....**2.6.2.3. *T.*** subgenus ***Discothesium***

**Note**: Subgenera are discussed according toour phylogenetic tree (Fig. 2.4). Species with an asterisk (*) are placed in the subgenus based on their geographical range and morphology. ≡ means homotypic names, = means heterotypic names and ~ means superfluous names.

### 2.6.2 Circumscription of subgenera

**2.6.2.1 *Thesium*** L. subgenus ***Hagnothesium*** (A.DC.) Zhigila, Verboom & Muasya, ***stat.nov.*** ≡ ***Thesium*** sect. *Hagnothesium* A.DC. in Esp. Nouv. *Thesium*: 4. 1857a – Type (designated by F.Forest & Manning in Bothalia, 43(2): 215. 2013): *Thesium fragile* L.f.

= *Thesidium* Sond.in Flora 40: 364. 1857a – Lectotype (designated by Pilger in A. Engler and K. Prantl, eds, 85. 1935): *Thesidium thunbergii* Sond. (= *T. fragile* L.f.).

*Diagnosis.* – Plant height < 50 cm, branching pattern virgate as in for example *T. fragile* or decumbent as in for example *T. microcarpum,* plant surface mostly glabrous, but scabrid species also present such as *T. hirtum*; leaf aspect well-developed or reduced to scale-like to

almost absent such as in *T. fragile* and allies, densely distributed on the plants, acicular or linear; floral bracts longer relative to flower length in *T. fruticulosum* and allies, but much shorter than flower in *T. fragile* and allies; inflorescences mostly spike, rarely 2-dichasial cymes, in branchlet axils, flower shape patelliform, perianth lobe apical trichomes absent, flower mostly 4-merous, although 5-merous taxa do occur such as *T. fragile* amidst 4-merous as teratological character, segments not distinctly uncinate, lobe segment inside colour green, outside colour green to yellowish-green, flowers unisexual; flowering throughout the year; fruit nutlets, green or white, ovoid or globose, dry or fleshy, persistent perianth segments green or orange, shorter than fruits.

*Species assigned* (8). – *Thesium fragile* L. (= *Thesidium thunbergii* Sond., *T. confusum* J.C.Manning and F.Forest, *T. podorcarpum* A.DC.), *T. fruticulosum* (A.W.Hill) J.C.Manning and F.Forest (= *Thesidium longifolium* A.W.Hill), *T. hirtum* (Sond.) Zhigila, Verboom and Muasya (= *Thesidium hirtum* Sond. *T. strigulosum* A.DC.), *T. leptostachyum* Sond. [= *Thesidium leptostachyum* (A.DC.) Sond.], *T. longicaule* Zhigila, Verboom and Muasya (*Thesidium longifolium* A.W.Hill, *T. longifolium* (A.W.Hill) J.C.Manning and F.Forest), *T. microcarpum* A.DC. (= *T. exocarpaeoides* Sond.), *T. minus* (A.W.Hill) J.C.Manning and F.Forest (= *Thesidium minus* A.W.Hill) and *T. quartzicolum* Zhigila, Verboom and Muasya

*Distribution.* – *Thesium* subgen. *Hagnothesium* are endemic to the GCFR, South Africa (Manning and Goldblatt, 2012; Forest and Manning, 2013). They are found along the coast on sand dunes or beach sand, as is the case for. *T. fragile*. Others such as *T. microcarpum* occur in shaly renosterveld scrub vegetation, sandstone mountain fynbos or quartz-silcrete substrates (Zhigila et al., 2019a, b).

*Notes.* – *Thesidium* Sond. was the name commonly used for this clade. The name was validly published by Sonder (1857a) at generic level, but in the same year Sonder (1857b) submerged it to *Thesium* and accorded it a sectional status to concur with De Candolle (1857a)'s treatment. Hill (1915) reinstated *Thesidium* to genus rank, and subsequent authors (*e.g.* Bobrov 1936, Hendrych, 1972) accepted this decision (Forest and Manning, 2013). De Candolle's (1857a) treatment of this clade as *Thesium* section *Hagnothesium* was resuscitated (Forest and Manning, 2013; Zhigila et al., 2019a) following the Shenzhen Code (Turland et al., 2018), but is here upgraded to subgeneric level.

**2.6.2.2 *Thesium*** L. subg. ***Thesium***, Sp. Pl.: 207: 1753 – Type: (designated by Hitchcock in Sprague, Nom. Prop. Brit. Bot.: 135. 1929): *Thesium alpinum* L., Mant. Pl. Altera: 213. 1771.

= *Thesium* sect. *Mauritanica* Batt. in Bull. Soc. Bot. France 35: 393. 1889 – Type: *Thesium mauritanicum* Batt. in Bull. Soc. Bot. France 35: 393. 1889.

= *Kunkeliella* Stearn in Cuad. Bot. Canaria 16: 17. 1972 – Type: *Kunkeliella canariensis* Skearn in Cuad. Bot. Canaria 16: 18. 1972.

= *Thesium* subg. *Chrysothesium* Jaub. & Spach in Ill. Pl. Orient. 2: ad. T. 104. 1844 ≡ *Thesium* sect. *Chrysothesium* (Jaub. & Spach) Walp. in Ann. Bot. Syst. 1: 581. 1849 ≡ *Chrysothesium* (Jaub. & Spach) Hendrych in Preslia 65: 319. 1994 – Type: *Thesium stelleroides Jaub. & Spach* in Ill. Pl.. Orient. 2: 1. 1844.

~ *Thesium* sect. "*Euthesium*" A.DC. in Candolle, Prodr. 14: 63. 1857, not validly published.

*Diagnosis.* – Plant height < 50 cm, branching pattern virgate such as in *T. chinense* or decumbent such as in *T. humile*, plant plant surface mostly glabrous, but scabrid species also present such as *T. mauritanicum*; leaf aspect well-developed, dense or moderately distributed on the plants, linear to lanceolate; floral bracts longer relative to flower length; inflorescences racemose or spike-like, in branchlet axils, flower shape patelliform or hypocrateriform, perianth lobe apical trichomes absent, flower mostly 5-merous, but 4-merous taxa do occur such as *T. alpinum* amidst 5-merous as teratological character, segments uncinate, lobe segment inside colour white, outside colour green, anthers below or in line with stigma; flowering time varies with species; fruit nutlet except in *T. subsucculentum*, where the fruits are drupes, green or white, except in *T. subsucculentum* and allies, ovoid or globose, dry or fleshy, persistent perianth segments green, shorter, equal or longer than fruit.

*Species assigned* (65). –*Thesium aellenianum* Lawalrée, *T. afghanicum* Hendr.*, *T. alatavicum* Kar. and Kir., *T. alpinum* L., *T. amicorum* Lawalrée, *T. annuum* Lawalrée*, *T. arvense* Horvatovszky (= *T. ramosum* Hayne), *T. aureum* Jaub. and Space.* [= *Chrysothesium aureum* (Jaub. and Spach) Hendr.], *T. auriculatum* Vandas, *T. australe* R.Br., *T. bavarum* Schrank, *T. bergeri* Zucc., *T. bomiense* C.Y.Wu*, *T. brachyphyllum* Boiss., *T. brevibracteatum* P.C.Tam*, *T. canariensis* (W.T.Stearn) J.C.Manning and F.Forest (≡ *Kunkeliella psilotoclada* (Svent.) W.T.Stearn), *T. catalaunicum* J.Pedrol and M.Laínz, *T. psilotocladum* Svent (= *K. psilotoclada* (Svent.) W.T.Stearn), *T. cathaicum* Hendr.*, *T. chimanimaniense* Brenan*, *T. chinense* Turcz., *T. cilicicum* Borm. [= *Chrysothesium cilicicum* (Jaub. and Spach) Hendr.], *T. corsalpinum* Hendr., *T. divaricatum* Jan ex Mert. and W.D.J.Koch *T. dolichomeres* Brenan*, *T. dollineri* Murb. *ex* Velen. (= *T. simplex* Velen), *T. emodi* Hendr. *, *T. erythronicum* Pamp. *, *T. himalense* Royle ap Edgew (= *T. thomsonii* Hendr.), *T. hispanicum* Hendr., *T. hookeri* Hendr*. (= *T. afghanicum* Hendr.), *T. humbertii* Cavaco and Keraudren, *T. humifusum* A.DC., *T. humile* Vahl (= *T. parnassi* A.DC., *T. graecum* Zucc.), *T. indicum* Hendr*. *T. impressum*

Steud. (= *T. kotschyanum* Boiss., *T. macranthum* Fenzyl, *T. rostratum* Mert. and W.D.J.Koch.), *T. jarmilae* Hendr.*, *T. kernerianum* Simonk.*, *T. krymense* Romo, Didukh and Borat.*, *T. linophyllon* L. (= *T. pratense* Ehrh.), *T. longiflorum* Handel-Mazzetti*, *T. longifolium* Turcz., *T. macedonicum* Hendrych*, *T. mauritanicum* Batt., *T. minkwitzianum* B.Fedtsch. [= *Chrysothesium minkwitzianum* (B.Fedtsch.) Hendr.], *T. multicaule* Hook.f. and Thomson ex A.DC., *T. orgadophilum* P.C.Tam*, *T. pachyrhizum* A.DC.*, *T. procumbens* C.A.Mey., *T. pyrenaicum* Pourr., *T. ramosissimum* Bobrov, *T. ramosoides* Hendr., *T. reekmansii* Lawalrée, *T. refractum* C.A.Meyer, *T. remotebracteatum* C.Y.Wu and D.D.Tao, *T. retamoides* (A.Santos) J.C.Manning and F.Forest (= *K. retamoides* A.Santos), *T. repens* Ledeb, *T. saxatile* Turcz. ex A.DC. *T. schmitzii* Robyns and Lawalrée, *T. setulosum* Robyns and Lawalrée, *T. stelleroides* Jaub. and Spach. [= *Chrysothesium stelleroides* (Jaub. and Spach) Hendr.], *T. subsucculentum* (Kämmer) J.C.Manning and F.Forest (= *K. subsucculenta* Kämmer), *T. tongolicum* Hendr.*, *T. vimineum* Robyns and Lawalrée, *T. wightianum* Wall.* (= *T. nilagiricum* Miq.).

*Distribution.* – *Thesium* subgen. *Thesium* is a clade with mainly Eurasian representatives drawn from Europe, East and Western Asia, Northwest Africa and the Canary Islands.

*Notes.* – The well-supported section *Thesium* encompasses all Eurasian taxa within which a previously erected section *Euthesium* (Pilger, 1935) and even subgenus *Chrysothesium* (Hendrych, 1994) are deeply embedded. The clade *Chrysothesium* was described as a section based on long perigonium and racemiform inflorescences (Bobrov, 1936). Also, species (*e.g. T. cilicicum, T. stelleroides* and *T. minkwitzianum*) included in this lineage are not monophyletic (Appendix Fig. S2.1). Hence, our phylogeny supports the data of Nickrent and García (2015) that lumped the *Chrysothesium* species into this clade. Moreover, of the first four species described by Linnaeus (1753), two species (*T. alpinum* and *T. linophyllon*) and the lectotype of the genus (*T. alpinum* L.) designated by Hitchcock (1929) were retrieved in this clade. Here, *Chrysothesium* has been reduced to a synonym in subgenus *Thesium* following the criteria of article 14 subsection 14.3 and article 22 subsection 22.1 of the International code of Botanical Nomenclature (Shenzhen Code, Turland et al., 2018).

**2.6.2.3** ***Thesium*** L. subg. ***Discothesium*** **(**A.DC.) Zhigila, Verboom & Muasya, ***stat. nov.*** **≡** *Thesium* sect. ***Discothesium*** A.DC. in Candolle, Prodr. Syst. Nat. XIV: 671. 1857 – **Type (designated here)**: *T. galioides* A.DC.

Of the two species, *Thesium galioides* and *T. planifolium* used by the original author (Candolle, 1857b) and cited in Hill (1915) within section *Discothesium*, *T. galioides* was chosen given that *T. planifolium* was synonymised under *T. triflorum*.

*Diagnosis.* – Plant height < 50 cm, branching pattern divaricate, intricate also occurs for example in *T. hystrix*, plant plant surface glabrous; leaf aspect well-developed, sparsely distributed on the plants, linear to lanceolate or reduced to scale-like; floral bracts shorter relative to flower length; inflorescence solitary flowers or dichasia (3-flowered cymes), in branchlet axils, flower shape patelliform, perianth lobe apical trichomes absent, flower mostly 5-merous, segments uncinate, lobe margins glabrous such as in *T. spinosum* or serrulate such as in *T. hystrix*, lobe segment inside colour white, outside colour green, anthers above stigma, although anthers below stigma do occur in, for example, *T. galioides*, flowering time varies with species; fruit nutlets, ovoid or globose, green, persistent perianth segment shorter than fruit, green.

*Species assigned* (15 species). – *Thesium cruciatum* A.W.Hill, *T. disciflorum* A.W.Hill*, *T. galioides* A.DC., *T. hystrix* A.W.Hill, *T. lacinulatum* A.W.Hill, *T. oresigenum* Compton, *T. pungens* A.W.Hill, *T. scandens* Sond., *T. spinosum* L.f., *T. spinulosum* A.DC. (= *T. aristatum* Schltr.), *T. squarrosum* L.f., *T. triflorum* Thunb. (= *T. planifolium* A.DC.), *T. virens* E.Mey., *T. whitehillensis* Compton and *T. xerophyticum* A.W.Hill (= *T. acathocladum* Schltr. and Pilg.).

*Distribution.* – species in *Thesium* subgen. *Discothesium* are southern African occurring from arid zones of Kalahari regions, Little Namaqualand in the North, the summer rainfall areas of the southwest and toward the Succulent Karoo mountains in Western Cape to Grahamstown in the Eastern Cape.

*Notes.* – the presence of disk-like flower characterising this clade made De Candolle (1857a) accord a sectional status (sect. *Discothesium*) to this group, which Hill (1915a) considered as a character insufficient to separate the clade and lumped the species into section *Imberbia*. Hill (1915b) placed *T. hystrix* and *T. horridum* in section *Imberbia* subsect. *Fimbriata* based on the long serrulate perianth lobe margins. Our phylogeny (Fig. 2.4) supports De Candolle's sectional treatment. Also, divaricate or intricate branching pattern, succulent leaves with spinous tips or entirely spiny are additional morphological characters to those used by De Candolle's (conspicuous flower disc) that unite this clade.

**2.6.2.4 *Thesium*** L. subg. ***Psilothesium*** (A.DC.) Zhigila, Verboom & Muasya, ***stat. nov.***

≡ *Thesium* sect. ***Psilothesium*** A.DC. in Candolle, Prodr. Syst. Nat. XIV: 670. 1857 ≡ *Austroamericium* Hendr. in Bol. Soc. Argent**.** Bot. 10: 126. 1963 – **Lectotype (designated here)**: *T. tepuiense* Steyerm.

The original concept of section *Psilothesium* was proposed by De Candolle (1857a, b), for the South American species to which *T. tepuiense* belongs, hence the choice as lectotype for this subgenus.

*Diagnosis.* – Plant height up to 100 cm, branching pattern intricate such as in *T. hystricoides*, decumbent or virgate such as in *T. costatum*, plant plant surface mostly glabrous or scabrid such as in *T. transvaalense*; leaf aspect well-developed, linear to lanceolate, densely or sparsely distributed on the plants to scale-like such as in *T. corymbuligerum* and allies; floral bracts longer or shorter relative than flowers; inflorescence types heteromorphic: racemose in *T. acutissimum* or cymose in *T. asterias* and allies or spikelets in *T. transvaalense*, rarely corymbose like in *T. corymbuligerum*, in branchlet axils or terminal head, flower shape patelliform, rarely hypocrateriform in *T. costatum*, perianth lobe apical trichomes present or absent, flower mostly 5-merous, but 4-merous, 6-merous or 7-merous do also occur as teratological characters, segments uncinate, lobe segment inside colour white, outside colour green, anthers below stigma in *T. tepuiense*, above or in line with stigma in rest; flowering time varies with species; fruit nutlets, green, ovoid or globose, dry, persistent perianth segments green shorter or equal, rarely longer than fruit.

*Species assigned* (98 species).– *Thesium acutissimum* A.DC., *T. alatum* Hilliard and B.L.Burtt., *T. angolense* Pilg.*, *T. angulosum* A.DC., *T. aphyllum* Mart. (= *T. tenuissimum* Hook.f.), *T. asterias* A.W.Hill, *T. atrum* A.W.Hill (= *T. quarrei* Robyns and Lawalrée), *T. bertramii* Aznav. *T. bequaertii* Robyns and Lawalrée, *T. brachyanthum* Baker*, *T. brasiliense* A.DC., *T. brevibarbatum* Pilg., *T. breyeri* N.E.Br.*, *T. bundiense* Hilliard*, *T. celatum* N.E.Br.*, *T. cinereum* A.W.Hill, *T. confine* Sond., *T. corymbuligerum* Sond., *T. costatum* A.W.Hill, *T. cupressoides* A.W.Hill, *T. cupressum* A.W.Hill, *T. cymosum* A.W.Hill* (= *T. fenarium* A.W.Hill, *T. nigricans* Rendle, *T. scabridulum* A.W.Hill), *T. davidsoniae* Brenan*, *T. dissitiflorum* Schltr., *T. dissitum* N.E. Br.*, *T. doloense* Pilg., *T. equisetoides* Welw. ex Hiern, *T. fanshawei* Hilliard*, *T. fastigiatum* A.W.Hill (= *T. luembense* Robyns and Lawalrée), *T. filipes* A.W.Hill, *T. fimbriatum* A.W.Hill (= *T. brachystylum* A.W.Hill, *T. stuhlmannii* Engl.), *T. fulvum* A.W. Hill*, *T. germanii* Robyns and Lawalrée, *T. gnidiaceum* A.DC., *T. goetzeanum* Engl. (= *T. caespitosum* Robyns and Lawalrée, *T. coriarium* A.W.Hill, *T. deceptum* N.E.Br., *T. laetum* Robyns and Lawalrée, *T. lewallei* Lawalrée, *T. macrogyne*

A.W.Hill, *T. nigrum* A.W.Hill, *T. orientale* A.W.Hill, *T. rhodesiacum* Pilg., *T. rogersii* A.W.Hill, *T. schaijeisii* Lawalrée, *T. gracile* A.W.Hill (= *T. palliolatum* A.W.Hill), *T. gracilorioides* A.W.Hill, *T. griseum* Sond., *T. gypsophiloides* A.W.Hill, *T. hockii* Robyns and Lawalrée, *T. horridum* A.W.Hill, *T. hystricoides* A.W.Hill, *T. impeditum* A.W.Hill (= *T. rasum* A.W.Hill), *T. infundibulare* N.Visser and M.M.le Roux, *T. inhambanense* Hilliard*, *T. inonoense* Hilliard* (= *T. bangweolense* R.E.Fr., *T. myriocladum* Baker ex A.W. Hill), *T. inversum* N.E.Br., *T. jeanae* Brenan*, *T. kilimandscharicum* Engl., *T. lesliei* N.E.Br.*, *T. leucanthum* Gilg.*, *T. libericum* Hepper and Keay*, *T. lobelioides* A.DC. (= *T. recurvifolium* Sond.), *T. lopollense* Hiern, *T. lycopodioides* Gilg., *T. madagascariense* A.DC., *T. magalismontanum* Sond., *T. magnifructum* Hilliard*, *T. masukense* Baker (= *T. matteii* Chiov., *T. whyteanum* Rendle), *T. moesiacum* Velen., *T. microphyllum* Robyns and Lawalrée, *T. mukense* Engl., *T. multiramulosum* Pilg. (= *T. pottiae* N.E.Br.), *T. myriocladum* Baker, *T. ovatifolium* N.Lombard and M.M.le Roux*, *T. pallidum* A.DC., *T. panganense* Polhill, *T. pawlowskianum* Lawalrée, *T. phyllostachyum* Sond., *T. pilosum* A.W.Hill*, *T. procerum* N.E.Br., Hilliard, T. *pseudocystoseiroides* Cavaco and Keraudren, *T. racemosum* Bernh. (= *T. gracilentum* N.E.Br.), *T. radicans* Hochst. ex A.Rich., *T. rectangulum* Welw.*, *T. pleuroloma* A.W.Hill, *T. polygaloides* A.W.Hill, *T. psilotoides* Hance, *T. pygmaeum* Hilliard*, *T. resedoides* A.W.Hill (= *T. burkei* A.W.Hill, *T. dumale* N.E.Br., *T. junodii* A.W.Hill, *T. mossi* N.E.Br., *T. welwitschii* Baum), *T. resinifolium* N.E.Br.*, *T. schweinfurthii* Engl., *T. schliebenii* L.f., *T. subaphyllum* Engl. (= *T. andongense* Hiern), *T. symoensii* Lawalrée, *T. szowitsii* A.DC., *T. tamariscinum* A.W.Hill, *T. tepuiense* Steyerm., *T. tetragonum* A.W.Hill (= *T. fuscum* A.W.Hill), *T. thamnus* Robyns and Lawalrée, (= *T. unyikense* var. *puberulum* R.E.fr.), *T. transvaalense* Schltr., *T. triste* A.W.Hill*, *T. ulugurense* Engl. (= *T. panganense* Polhill), *T. utile* A.W.Hill, *T. vahrmeijeri* Brenan, *T. viride* A.W.Hill (= *T. hararensis* A.G.Mill., *T. unyikense* Engl)., *T. wilczekianum* Lawalrée, *T. zeyheri* A.DC. (= *T. longirostre* Schltr.).

*Distribution.* – Southern Africa, tropical and subtropical Africa, Madagascar and tropical South America.

*Notes.* – subgenus *Psilothesium* was described as a section by De Candolle (1857b) from which Hendrych (1963) segregated the South American species into the genus *Austroamericium* based on significant geographical isolation pattern. Subsequent molecular phylogenetic studies (Moore et al., 2010; Nickrent and García, 2015; García et al., 2018) did not support this separation and *Austroamericium* species were merged into the mainly tropical African clade *Psilothesium*, bringing together plants occurring in the tropics. Recent taxonomic revision of the *T. goetzeanum* complex (Visser et al., 2018; grassland species) clarified some

species limits and nomenclature.

**2.6.2.5 *Thesium* L.** subgenus ***Frisea*** (Rchb.) Hendrych in Acta Univ. Carol., Biol. 1970: 341: 1972 ≡ Thesium sect. Frisea Rchb., Consp. Reg. Veg.: 80. 1828 – Type: *Thesium frisea* L., Mant. Pl. Altera: 213. 1771.

*Diagnosis.* – Plant height < 50 cm such as in *T. virgatum* and allies, to about 100 cm in *T. aggregatum*, or up to 250 cm tall in *T. strictum* and allies, branching pattern polymorphic: virgate in *T. carinatum* and allies, intricate in *T. archeri* to decumbent

in *T. prostratum,* plant plant surface mostly glabrous or scabrid such as in in *T. scabrum* and allies; leaf aspect well-developed, linear to lanceolate, densely distributed in *T. viridifolium* and allies or sparsely distributed on the plants. in *T. funale* and allies to scale-like in *T. nigromontanum* and allies; floral bracts shorter or equal to longer relative to flower length; inflorescence types heteromorphic: mostly spikelets, axillary to elongated or globose terminal heads, 3-flowered cymes, to corymbose such as in *T. helichrysioides* and allies, rarely racemose like in *T. glomeratum* or solitary in *T. euphrasioides* and allies, flower shape patelliform in *Imberbia* species like *T. nudicaule* and allies or hypocrateriform as in *Barbata* clade, as in *T. karooicum* or urceolate as in *T. urceolatum*, perianth lobe apical trichomes present in subclade *Frisea* or absent in *T. ericaefolium* and allies, flower mostly 5-merous, while 4-merous, 6- merous or 7-merous do occur amidst 5-merous as teratological characters, segments uncinate or indistinct, lobe segment inside colour white, outside colour green, anthers above stigma, rarely in line with, but never below stigma; flowering time varies with species; fruit nutlets, green, ovoid or globose, dry, persistent perianth segments green, shorter or equal, rarely longer than fruit.

*Species assigned* (103). – *Thesium abietinum* Schltr.*, *T. acuminatum* A.W.Hill, *T. aggregatum* A.W.Hill, *T. albomontanum* Compton, *T. annulatum* A.W.Hill, *T. archeri* Compton (= *T. marlothii* Schltr.), *T. aspermontanum* Zhigila, Verboom and Muasya, *T. bathyschistum* Schltr., *T. boissierianum* A.DC.*, *T. brachygyne* Schltr., *T. burchellii* A.W.Hill* (= *T. megalocarpum* A.W.Hill), *T. capitatum* L., *T. carinatum* A.DC., *T. capitellatum* A.DC., *T. capituliflorum* Sond., *T. commutatum* Sond., *T. congestum* R.A.Dyer*, *cornigerum* A.W.Hill*, *T. cuspidatum, T. cytisoides* A.W.Hill, *T. densiflorum* A.DC., *T. dinteri* A.W.Hill, *T. diversifolium* Sond., *T. dmmagiae* Zhigila, Verboom and Muasya, *T. durum* Hillard and B.L.Burtt., *T. ecklonianum* Sond., *T. elatius* Sond., *T. ericaefolium* A.DC., *T. euphorbioides* L. (= *T. amplexicaule* Linn.), *T. fallax* Schltr., *T. flexuosum* A.DC., *T. floribundum* A.W.Hill*, *T. foliosum* A.DC., *T. frisea* Sond. (= *T. amblystachyum* A.DC.), *T. fructicosum* A.W.Hill, *T.*

*funale* L. (= *T. adpressifolium* Sond.), *T. glaucescens* A.W.Hill*, *T. glomeruliflorum* Sond., *T. helichrysioides* A.W.Hill, *T. helodes* Hilliard, *T. hillianum* Compton, *T. hispidulum* Lam. (= *T. hispidum* Schltr.), *T. hispidulum* Lam. var. *subglabra* A.W.Hill *(T. conostylum* Schltr.), *T. hollandii* Compton, *T. imbricatum* Thunb., *T. junceum*, *T. juncifolium* A.DC., *T. karooicum* Compton, *T. katangense* Robyns and Lawalrée*, *T. leptocaule* Sond., *T. lisae-mariae* Stauffer, *T. litoreum* Brenan, *T. macrostachyum* A.DC., *T. microcephalum* A.W.Hill, *T. micromeria* A.DC., *T. micropogon* A.DC., *T. namaquense Schltr., T. natalense* Sond., *T. nautimontanum* M.A. García, Nickrent and Mucina, *T. neoprostratum* Zhigila, Verboom and Muasya, *T. nigroperianthum* Zhigila, Verboom and Muasya, *T. nigromontanum* Sond., *T. nudicaule* A.W.Hill, *T. occidentale* A.W.Hill, *T. paniculatum* L., *T. paronycoides* Sond., *T. patulum* A.W.Hill, *T. pinifolium* A.DC., *polycephalum* Schltr., *T. penicillatum* A.W.Hill, *T. prostratum* A.W.Hill, *T. pseudovirgatum* Levyns, *T. pubescens* A.DC., *T. pycnanthus* Schltr., *T. quinqueflorum* Sond. (= *T. erectiramosum* A.DC., *T. affine* Schltr.), *T. rariflorum* Sond (=*T. maximiliani* Schltr.), *T. repandum* A.W.Hill, *T. rhizomatum* Zhigila, Verboom and Muasya, *T. robynsii* Lawalrée*, *T. rufescens* A.W.Hill (= *T. hispidum* Schltr.), *T. sawae* Zhigila, Verboom and Muasya, *T. scabrum* L., *T. schumannianum* Schltr., *T. scirpioides* A.W.Hill, *T. sedifolium* A.DC. ex Levyns (= *T. crassifolium* Sond.), *T. selagineum* A.DC. *T. semotum* N.E.Br., *T. sertulariastrum* A.W.Hill, *T. sondarianum* Schltr., *T. spartioides* A.W.Hill, *T. spicatum* L., *T. stirtonii* Zhigila, Verboom and Muasya, *T. strictum* P.J.Bergius., *T. subnudum* Sond., *T. subsimile* N.E.Br., *T. sussanae* A.W.Hill, *T. singulare* Thunb*., *T. transluscens* A.W.Hill., *T. urceolatum* A.W.Hill (= *T. exile* N.Br.), *T. ussanguense* Engl. (= *T. passerinoides* Robyns and Lawalrée, *T. scoparium* Peter), *T. schlechteri* A.W.Hill, *T. virgatum* Lam. *T. viridifolium* Levyns.

*Distribution.* – All species occur in the GCFR, South Africa. Although some species such as *T. hillianum* do extend their ranges into tropical and subtropical regions.

*Notes.* – Hill (1915; 1925) proposed a sectional classification for South African species, including the sections *Barbata* (species with apical trichomes on the perianth lobes), *Imberbia* including subsection *Subglabra* and subsection *Fimbriata* (species without apical trichomes on the perianth lobes). However, Hendrych (1972) upheld the previous (Reichenbach, 1828 and Bobrov, 1936) classification by dividing subgenus *Frisea* into sections *Frisea*, *Barbata* and *Penicillata*. In this study, although the subgenus *Frisea* is strongly supported, there is no single unequivocal morphological character unique to all species in this clade. Anthers exserted or inserted above stigma might have been a uniting trait, but anthers are also found in line with the stigma in some species such as in *T. viridifolium.*

# CHAPTER THREE

## 3.0 A taxonomic revision of *Thesium* subgenus *Hagnothesium* (Santalaceae) and description of a new species, *T. quartzicolum*

### 3.1 Introduction

Recent molecular phylogenetic studies (Moore et al., 2010; Nickrent and García, 2015; García et al., 2018; Chapter 2) provided the foundation for the first monophyly-based infrageneric classification of *Thesium*, leading to the recognition of clades with strong biogeographic patterns (Nickrent and García, 2015; Fig. 3.1). The monophyly of the *Hagnothesium* clade is well-supported as is that of its two component subclades (Zhigila et al., 2019a; Chapter two; Fig. 3.1). The *Hagnothesium* clade, sister to the South African/Eurasian clade (Moore et al., 2010; Nickrent and García, 2015; Fig. 3.1A), is endemic to the Greater Cape Floristic Region (GCFR) (Manning and Goldblatt, 2012). The GCFR is characterized by variable relief, geology and climate (Bradshaw and Cowling, 2014) and long-term climatic stability (*e.g.* Cowling and Lombard, 2002), and these factors have been invoked to explain its remarkable concentrations of locally-endemic species (Goldblatt and Manning 2000; Cowling and Lombard, 2002; Manning and Goldblatt, 2012). Within this region most members of the subgenus *Hagnothesium* occur along the coast and in/amongst mountain Fynbos, Strandveld and Renosterveld vegetation (Hill, 1925). Species of the subgenus *Hagnothesium* were distinguished from other species of *Thesium* based on their dioecious reproductive system, four-merous flowers and all-year flowering (Manning and Goldblatt, 2012).

The concept of *Hagnothesium* adopted here follows from the work of Alphonse de Candolle (1857a) who segregated *Thesium fragile* L.f., along with five newly-described species, *T. globosum* A.DC., *T. leptostachyum* A.DC., *T. microcarpum* A.DC., *T. podocarpum* A.DC. and *T. strigulosum* A.DC., as *Thesium* subgenus *Hagnothesium* based on their dioecious breeding system and four-merous flowers. In the same year, Sonder (1857a) independently described several of these same species, applying different names, but segregating them as a distinct genus, *Thesidium*. Thus, for example, *Thesidium exocarpaeoides* Sond. was applied to *Thesium microcarpum*, *Thesidium thunbergii* Sond. to *Thesium podocarpum*, and *Thesidium hirtum* Sond. to *Thesium strigulosum* (Hill, 1925). The concurrent treatment of this clade by both De Candolle and Sonder generated taxonomic confusion, which was further exacerbated by Sonder's (1857b) subsequent decision to downgrade his genus *Thesidium* to *Thesium* section *Thesidium* (Forest and Manning, 2013). Additional confusion arose, because some species were described based on female plants alone; a different name being applied to male material of the

same species. For example, *T. globosum* and *T. strigulosum* respectively represent a male and a female plant of the same species, which Sonder (1857a or b) correctly unified under the name *T. hirtum* (Hill, 1915b).

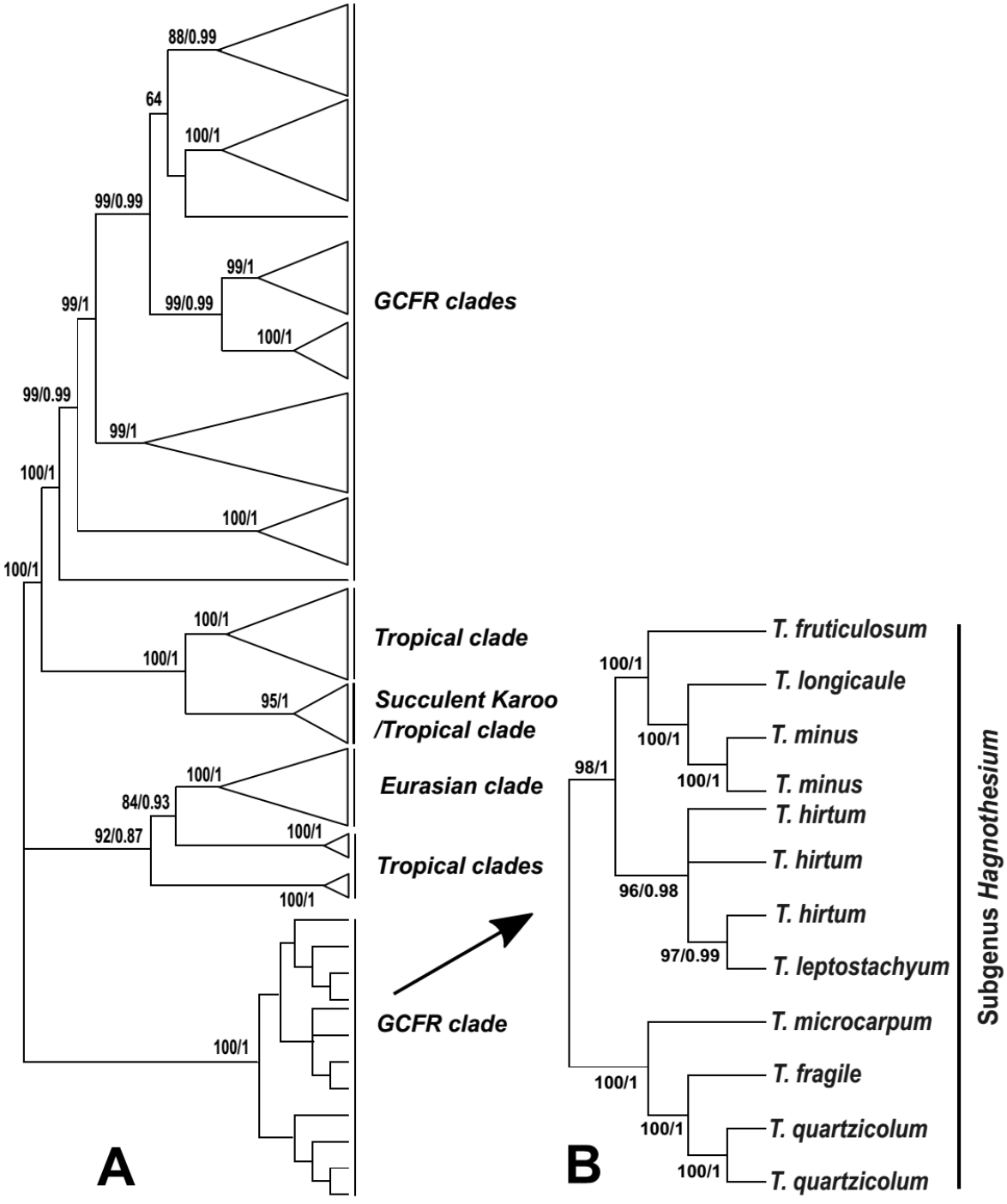



**Fig. 3.1:** (A) Reconstruction of the phylogenetic tree of *Thesium* based on ITS, matK, rpl32 trnF(UAG) and trnL-trnF sequence data (adapted and modified from Moore et al., 2010, Nickrent and García, 2015; Chapter two) indicating the monophyly of the subgenus *Hagnothesium*.

Following Sonder (1857a) and Hill (1925) treatment of species in subgenus *Hagnothesium* as a separate genus, *Thesidium*, aligning existing names accordingly and described three additional species: *Thesidium fruticulosum* A.W.Hill, *Thesidium longifolium* A.W.Hill and *Thesidium minus* A.W.Hill (Hill, 1925). Subsequent authors such as Pilger (1935) and Hendrych (1972) followed Hill (1925)'s nomenclatural treatment of *Thesidium*, probably because they were unable to study the South African taxa thoroughly (*e.g.* Hendrych, 1972). On the recommendation of Moore et al. (2010), however, and following the principle of taxonomic monophyly (Schrire and Lewis, 1996; Backlund and Bremer, 1998; Humphreys and Linder, 2009), Forest and Manning (2013) recently collapsed the genus *Thesidium*, together with *Kunkeliella* W.T.Stearn, into *Thesium*, but accorded sectional status to both.

Although Forest and Manning (2013) made the necessary nomenclatural changes to species in the aforementioned taxa, they did not assess species boundaries. Problems remained that needed to be clarified. Firstly, species included in subgenus *Hagnothesium* were last revised almost a century ago, with the result that the current taxonomy is out of date given recent taxonomic alignments (Forest and Manning, 2013). Secondly, in this context, species diagnoses based on Hill's (1925) work remain problematic as uncertain species circumscriptions still exist and, given the accumulation of new collections in herbaria, a revision of species limits was much needed. Thirdly, many species of *Thesium* and *Thesidium* are considered data deficient in terms of their taxonomy and conservation status (Raimondo et al., 2009; Von Staden, 2015), such that *Thesium* has been identified as a priority for taxonomic research by the South African National Strategy (Victor et al., 2015). Fourthly, the Plant List (2019) enumerated 15 scientific names for *Thesidium*, of which nine are unresolved.

The objectives of this chapter were therefore: (i) to reassess species boundaries within the *Hagnothesium* clade by the application of standard univariate and multivariate morphometric approaches to herbarium materials representing the full suite of previously recognized species and a putative new species; (ii) to determine the appropriate current name, synonymy and typification for each included species,; (iii) to provide a nomenclatural synopsis, a formal description, an illustration, a map of its geographical range, an ecological assessment and an updated conservation status for each species; and (iv) to produce a technical key for species identification.

## 3.2. Materials and Methods

### 3.2.1. Data collection

Observations were based on a total of 342 herbarium specimens housed at BOL, FHO, HPG, K, MO, NBG, OXF (including SAM and STE), PH, PRE, S and WU (acronyms following Thiers, 2019), as well as plants seen growing in their natural habitats during large-scale field surveys during 2007 to 2019. In addition, we studied high-resolution images of types and isotypes from JSTOR Global Plants (JSTOR, 2018) and other online images, such as Phytoimages (2019). For the morphometric analysis, characters were scored from a representative sample of specimens of each species (wherever possible, at least 10 accessions), ensuring that geographical range and morphological variability of each species was covered. Where necessary, observations were done using a stereomicroscope (Nikon Stereoscopic Zoom Microscope SMZ1500 fitted with Nikon DS-5M Camera). A scanning electron microscope (SEM, The Phenom™ proX desktop) was used for an ultrastructural study of stem and leaf epidermal traits. Additional specimens collected during field trips for this study were deposited at BOL, with duplicates distributed to K, NBG and PRE. The nomenclatural treatment follows the principles outlined in the Shenzhen Botanical Code (Turland et al., 2018).

### 3.2.2 Distribution maps

Specimen localities were obtained from herbarium records and our field collections. Misidentifications of species were common given the lack of clear-cut characters and the small size of many plant traits in *Thesium*, but these were verified individually against type specimens. Of the 342 specimens studied, 153 contained coordinates or at least referred to quarter degree grid cells, 166 contained precise locations that were queried against Google My Map of South Africa to obtain the coordinates, while the remaining specimens could not be used for mapping. Distribution maps were generated on specimen localities using the raster package version 2.6-7 (Hijmans, 2017) as implemented in R version 3.5.1 (R Team, 2018) based on biome and topographical maps (Leister and Morris, 1976).

### 3.2.3 Conservation assessment

The red list status for each species followed Raimondo et al. (2009), Von Staden (2015) and amendments to the existing and new statuses were made using the guidelines of the International Union for Conservation of Nature (IUCN, Standards and Petitions Subcommittee, 2017).

### 3.2.4 Statistical analyses

The data set used for morphometric analysis contained 30 discrete and 19 continuous traits (Appendix Table S3.1). Simple boxplots, as implemented in R version 3.5.1 (R Team, 2018), were used to compare the variation of individual continuous characters between species and to check for variation gaps between species. In addition, multivariate pattern was assessed using Principal Component Analysis (PCA, in which only quantitative continuous traits were used) and Principal Coordinate Analyses (PCoA) as applied to a matrix of pairwise Gower distances (Gower, 1971). The latter was determined using the package 'gower' version 0.1.2 (van der Loo, 2017) in R, which determines the quantitative trait distance as the mean character difference and the qualitative trait distance as the additive inverse of the simple matching coefficient (Gower, 1971). Quantitative trait distances were based on z-standardized values (using the package 'daisy' in R) of each trait to ensure that traits contributed equally to the analysis. Although PCoA can integrate categorical and numeric variables (Sassone et al., 2013), it does not consider variations within closely related specimens (Everitt et al., 2011). To compensate for this, cluster analyses using the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) algorithm was performed in R, as this is a better estimate of similarity relationships amongst closely related species (Chandler and Crisp, 1998).

## 3.3. Results

### 3.3.1 Morphology

Morphological characters common to all species in subgenus *Hagnothesium* include (i) leaves decurrent; (ii) plants dioecious; (iii) flowers four-merous (rarely five-merous); (iv) flower shape campanulate; (v) flowers in axillary spikes, rarely two to three dichasia; (vi) the lobe segments free to the hypanthium; (vii) hypanthium tube short to non-existent; and (viii) persistent perianth segments shorter than the fruits (Fig. 3.2). These characters were consistently invariant across species, and hence excluded from all subsequent analyses.

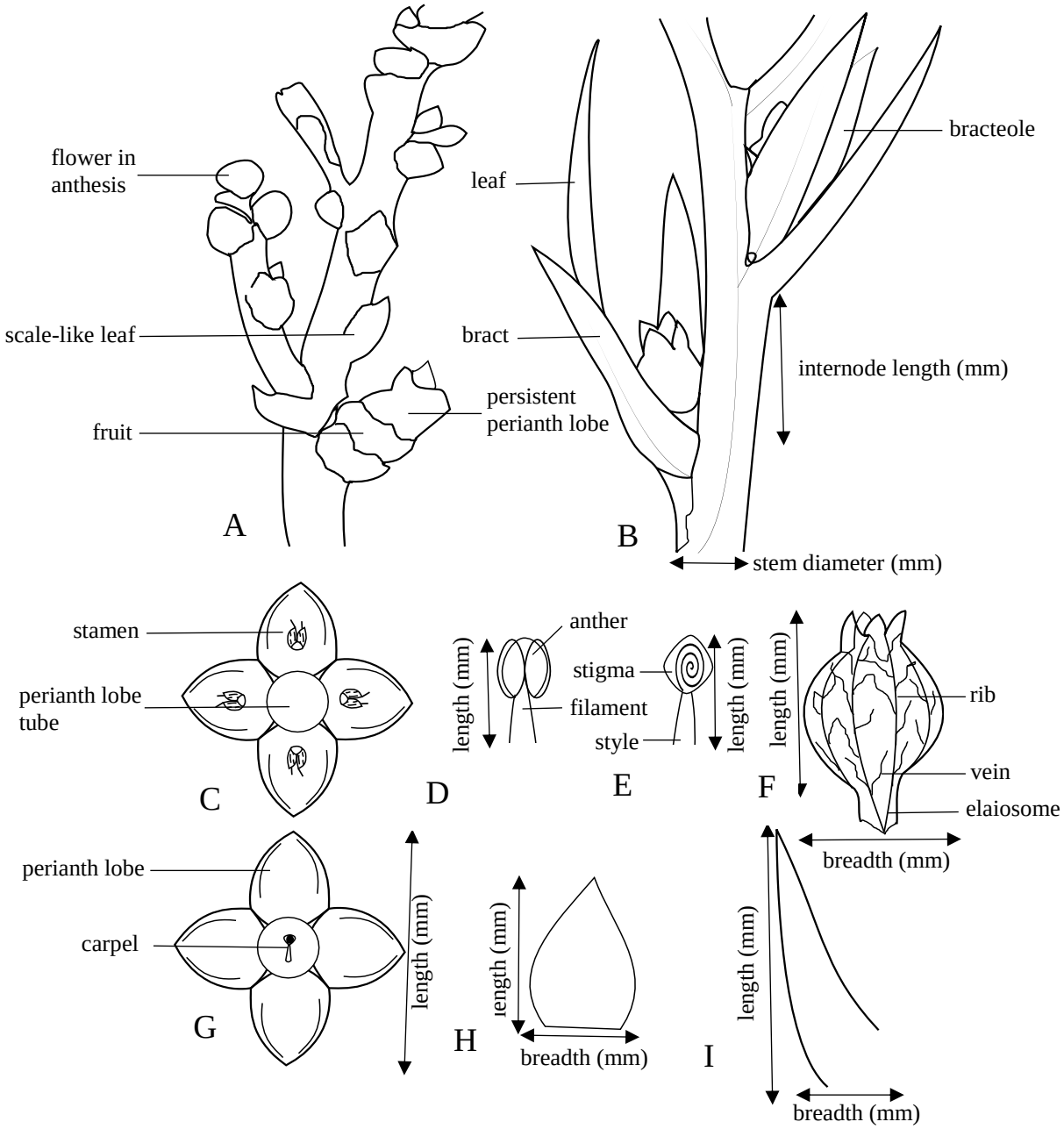



**Fig. 3.2:** Illustrations to aid interpretation of some vegetative and reproductive characters used for descriptions of species in subgenus *Hagnothesium*: (A) a typical twig of species with reduced vegetative traits, flowers and fruits such as *T. fragile* and allies, (B) a typical twig of species with long vegetative and reproductive traits such in *T. hirtum* and allies, (C) a male flower with four perianth lobes and stamens, (D) filament and anther, (E) style and stigma, (F) a fruit, (G) a female flower, (H) a perianth lobe, (I) a leaf. ⟷ indicates distances measured (mm) on specimens.

Assessments of which traits best distinguish species are presented as a series of box-and-whisker plots (Fig. 3.3). The univariate analysis of the continuous morphological data revealed clear separation of the species with respect to overall morphology, except of *Thesidium thunbergii* versus *T. fragile*, in which characters overlapped (Fig. 3.3). Characters such as leaf and bract length in both male and female plants separate species in subgenus *Hagnothesium* into two distinct natural groups, *T. fruticulosum, T. longicaule, T. minus* and *T. hirtum* with longer leaves, bracts and bracteoles, and *T. quartzicolum, T. fragile* and *T. microcarpum* with short (or reduced to scale leaves) bracts and bracteoles (Fig. 3.3A–D). Other characters that helped to identify breaks in species boundaries included plant height, stem diameter, internode distance, perianth lobe dimensions and flower size (Fig. 3.3E– L).

### 3.3.2 Growth habit

The species in subgenus *Hagnothesium* are perennial shrubs, suffrutices or annual herbs with perennial roots or rhizomes (Table 3.1); Species in the subgenus *Hagnothesium* are heath-like (*in T. quartzicolum T. hirtum* and *T. fragile*) or grow under other shrubs (in *T. microcarpum, T. fruticulosum,* and *T. minus*), 5–40 cm tall (Fig. 3.3G), with a virgate, sprawling or fastigiate branching pattern (Table 3.1). In overall appearance, the male and female plants of the same species are mostly very dissimilar in *T. hirtum* and allies, making it relatively easy to match male and female plants of the same species. In *T. fragile* and allies, however, the male and female plants of different species are indistinct, and without evidence from collection sites (in which mostly both male and female plants occupy the same locality), it is difficult to assign male plants to the appropriate female plants of the same species.

### 3.3.3 Vegetative traits

Species such as *T. fragile* and allies are yellowish to golden-green in general appearance, have stems that are brittle, especially when dry, and terete or sulcate in transverse section (Table 3.1). Conversely, in species such as *T. hirtum* and allies, the plants are yellowish-green in general appearance, stems are not brittle, exclusively sulcate in transverse section, and glabrous or have short hispid structures on the stem ridges, especially in *T. hirtum* and *T. longicaule* (Table 3.1). Leaves distinguish the species of the subgenus *Hagnothesium* in two ways. In *T. fragile* and allies, leaves are highly-reduced to scale-like (0.5–2.5 mm long), triangular, somewhat fleshy without a prominent midrib, suborbicular at the base and have

entire to cartilaginous margins. In contrast, leaves in species such as *T. hirtum* and allies are well-developed (elongate), varying from linear to lanceolate or acicular. In most cases, the male plants have smaller (1–6 mm; versus 5.6–15 mm in females), lanceolate and imbricate leaves, an exception being *T. longicaule* in which the male plants have longer (5–10 mm), acicular leaves that give them a distinct appearance compared to their female counterparts. The leaf margins are entire or membranous in *T. fruticulosum* and allies (except in *T. hirtum* in which the leaf margins are scabridulous), the midribs are prominently raised, concave or straight (Table 3.1).

The internode is a taxonomically important trait among species in the subgenus *Hagnothesium*. *Thesium longicaule, T. fragile* and *T. quartzicolum* all have long internodes in both male (Fig. 3.3F; 3–13 mm) and female (Fig. 3.3E; 1.3–13.0 mm) plants. Conversely, *T. hirtum* and *T. fruticulosum* have short (0.5–4.0 mm) internodes in both male and female plants (Fig. 3.3F).

Bracts and bracteoles subtend the branchlets on which inflorescences are borne in species of the subgenus *Hagnothesium* (Fig. 3.2). The bracts are smaller and thinner than the bracteoles and their lengths provided two natural distinctions for species within the section (Fig. 3.3A and D). The leaf-like bracts and bracteoles are characteristic traits of *T. hirtum* and allies, whereas in *T. fragile, T. microcarpum* and *T. quartzicolum* have scale-like bracts. Also, bracts and bracteoles are much longer relative to the flower length in *T. hirtum* and allies, but much shorter in *T. fragile* and allies.

### 3.3.4 Reproductive traits

Some variation in floral traits were found among species in the subgenus *Hagnothesium*. For instance, *T. quartzicolum*, *T. minus* and *T. microcarpum* have longer (2–5 mm) flowers than *T. fragile*, *T. fruticulosum*, *T. hirtum* and *T. longicaule* (0.7–2 mm long) (Fig. 3.3I). Other characters vary among individuals of the same species, such as perianth lobe shape, perianth size (Fig. 3.3K and L) and flower breadth (Fig. 3.3J), with male and female flowers of the same species often showing differences. Male flowers are typically campanulate, with subulate lobe segments; four anthers, two locules, staminal filaments are exserted beyond the walls of perianth lobes at the junction with the hypanthium, short (0.2–0.4 mm); hypanthium tube short to non-existent, shorter than the perianth lobe segments. *Female flowers* have short or absent pedicels, which, if present, swells to form an ovoid or truncate elaiosome at maturity; the perianth lobe segments are ovate to lanceolate; ovary inferior and short with a 2–3 lobed stigma (Hill, 1925) and a straight or curved placenta.

The fruits are generally small (1.3–3.4 × 1–3.2 mm, Table 3.1) ovoid or globose nutlets, with the exception of *T. fragile* whose fruits are truncated (Fig. 3.2). The short to non-existent pedicel may be swollen to form an elaiosome, which is attenuated toward the point of attachment or circular in shape. The fruit surfaces of species in subgenus *Hagnothesium* are generally 10-ribbed, although 5-ribbed fruit surfaces have been observed in *T. fragile* or ribs may be absent as in *T. microcarpum*. Between the ribs, if present, are reticulate anastomosing veins, but species without ribs lack prominent veins. The fruits are usually capped by persistent perianth segments that are shorter than the fruits. Slight differences exist among species in the colour and length of the perianth remnants. In *T. fragile* the perianth remnants are green when young, but gradually turn yellowish and then orange with maturity. In the remaining species, the perianth remnants remain green (Table 3.1).

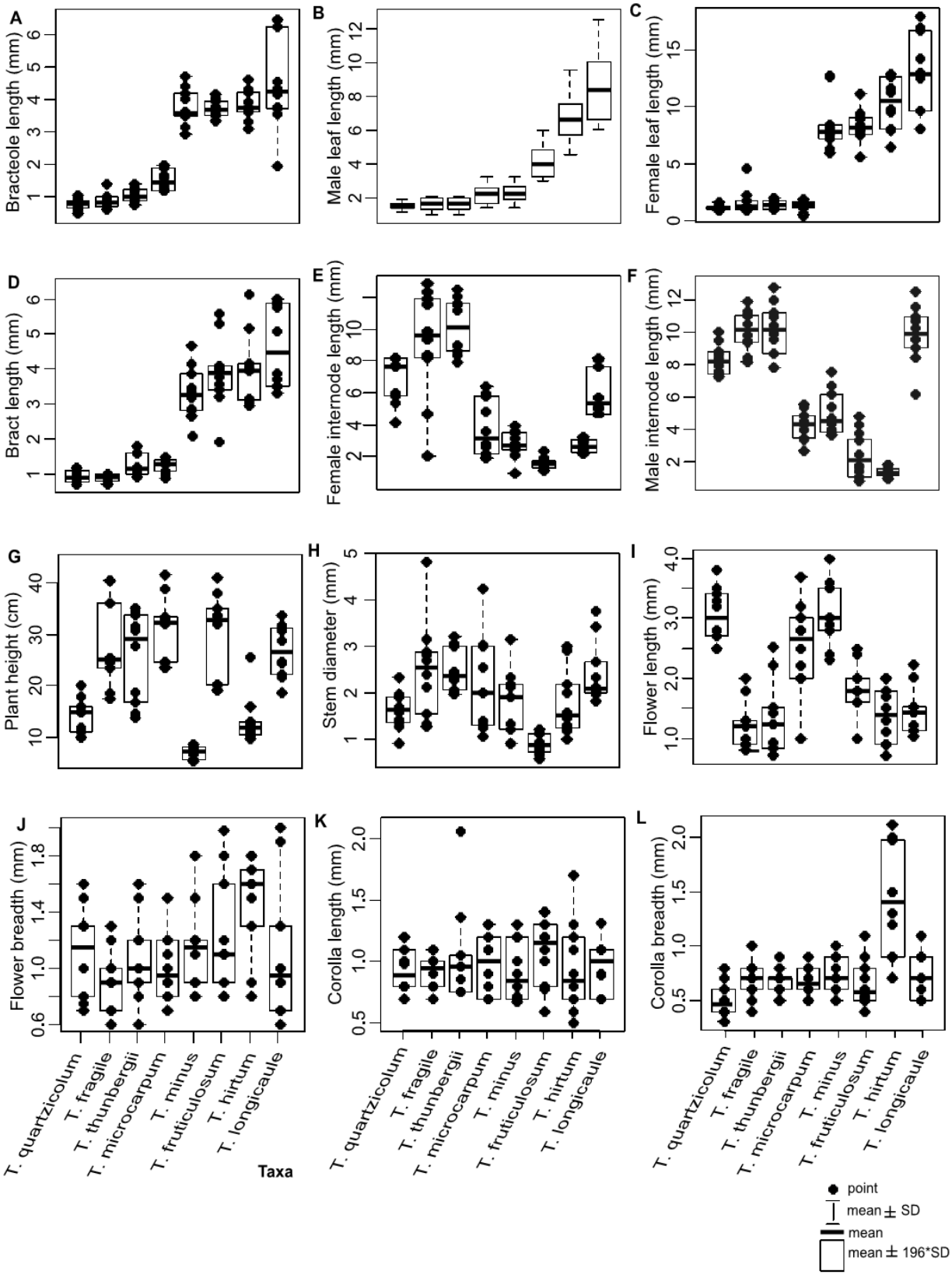



**Fig. 3.3 (A−L):** Box and whisker plots of twelve discrete characters that showed variation among the specimens in the subgenus *Hagnothesium*.

**Table 3.1:** A summary of morphological and ecological traits used to delimit members of *Thesium* subgenus *Hagnothesium.* Question mark (?) indicates unavailable data.

| | *T. fragile* | *T. fruticulosum* | *T. hirtum* | *T. leptostachyum* | *T. longicaule* | *T. microcarpum* | *T. minus* | *T. quartzicolum* |
|---|---|---|---|---|---|---|---|---|
| Life form | perennial | perennial | perennial | annual | perennial | perennial | annual | annual |
| Growth exposure | heath–like | under shrubs | under shrubs | ? | heath–like | under shrubs | under shrubs | heath–like |
| Male and female plants | similar | dissimilar | dissimilar | ? | dissimilar | similar | dissimilar | similar |
| Root system | woody taproot | slender fibrous | slender fibrous | ? | slender fibrous | slender fibrous | rhizome fibrous | slender fibrous |
| Plant height (cm) | 21–40 | 18–31 | 9–25 | ? | 20–30 | 22–38 | 5–10 | 8–15 |
| Plant surface | gabrous | glabrous | scabrid | glabrous | subglabrous | glabrous | glabrous | glabrous |
| Stem diameter (mm) | 1.3–4 | 2–3.5 | 1–3 | ? | 1–3 | 0.9–3 | 0.5–1.2 | 1.3–3 |
| Stem transverse section | sulcate | sulcate | sulcate | sulcate | sulcate | terete | sulcate | terete |
| Branching pattern | virgate | fastigiate | virgate | ? | virgate | fastigiate | fastigiate | virgate |
| Number of branches | 4–10 | 5–15 | 4–12 | ? | 3–12 | 5–12 | 4–12 | 3–10 |
| Branch distribution | sparingly | dense at basal portion | dense at basal portion | ? | sparingly | dense at distal portion | dense at basal portion | sparingly |
| Male internode length (mm) | 8–12 | 0.5–4 | 0.7–1.6 | 0.5–3 | 4–10 | 2–6.5 | 2.5–8 | 3–6.5 |
| Female internode length (mm) | 2–13 | 0.5–3 | 0.7–1.5 | ? | 1–5 | 3.5–7.5 | 1.5–2.5 | 4–8 |
| Leaf shape | scale–like to absent | linear | lanceolate | lanceolate | acicular | scale–like to absent | linear | scale–like |
| Leaf density at base | sparse | dense | dense | ? | dense | sparse | dense | sparse |
| Male leaf length (mm) | 1–2.5 | 3–5.3 | 2.4–6 | ? | 5–10 | 1–2 | 2–6 | 1–2 |
| Female leaf length (mm) | 1–2.2 | 5.6– 10 | 6–12.7 | ? | 8–17.93 | 0.5–1.5 | 7.5–12.8 | 1–1.5 |
| Male leaf breadth (mm) | 0.6–1.2 | 0.5–1.1 | 0.5–1.5 | ? | 0.4–0.8 | 0.6–1.2 | 0.5–1 | 0.5–0.8 |
| Female leaf breadth (mm) | 0.5–1.2 | 1—3 | 1–2.3 | ? | 0.5–1.5 | 0.5–1.2 | 0.2–0.9 | 0.5–0.8 |
| Leaf midrib | not raised | raised | not raised | not raised | raised | not raised | not raised | not raised |
| Leaf margin | entire or cartilaginous | entire | scabrid | entire | entire | entire | entire | cartilaginous |
| Leaf margin texture | cartilaginous | not cartilaginous | cartilaginous | ? | cartilaginous | not cartilaginous | not cartilaginous | cartilaginous |
| Bract shape | triangular | lanceolate | lanceolate | ? | lanceolate | lanceolate | lanceolate | triangular |
| Bract midrib aspect | not raised | not raised | raised | ? | not raised | not raised | raised | not raised |
| Bract length (mm) | 0.7–1.5 | 2–6.4 | 1.8–5 | ? | 5–10 | 1–1.5 | 2.5–5.3 | 0.8–3 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Bract breadth (mm) | 0.5–1.3 | 1–2 | 1.2–2.9 | ? | 2–2.5 | 0.4–1 | 0.5–1.2 | 0.8–2.3 |
| Bracts and bracteoles | scale–like | leaf–like | leaf–like | leaf–like | leaf–like | scale–like | leaf–like | scale–like |
| Bracteole shape | triangular | lanceolate | linear | triangular | linear | triangular | lanceolate | triangular |
| Bracteole length (mm) | 0.5–1.2 | 1.1–4.2 | 1.1–3.2 | ? | 3–4.2 | 0.6–1 | 1.5–3.2 | 0.7–2.5 |
| Bracteole breadth (mm) | 0.4–1.2 | 0.8–2 | 0.5–2.5 | ? | 0.5–2 | 0.3–1 | 0.5–1.5 | 0.5–1.6 |
| Bracteole texture | thick | thin | thick | thick | thin | thick | thin | thin |
| Bracteole midrib | raised | raised | raised | not raised | not raised | not raised | raised | not raised |
| Bracteole margin texture | entire | entire | scabrid | ? | entire | entire | entire | serrated |
| Bract/flower length | shorter than flower | longer than flower | longer than flower | longer than flower | longer than flower | shorter than flower | longer than flower | shorter than flower |
| Flower length (mm) | 0.8–2 | 1–2.5 | 0.7–2 | ? | 2–3.7 | 2.3–4 | 1–2.5 | 2.5–5 |
| Flower breadth (mm) | 0.6–2 | 0.8–1.5 | 0.8–1.8 | ? | 0.7–1.5 | 3.8–4.8 | 0.5–1.3 | 2.2–4 |
| Perianth lobe shape | triangular | triangular | lanceolate | ? | lanceolate | ovate | lanceolate | triangular |
| Perianth lobe length (mm) | 0.5–1 | 0.5–1.2 | 0.5–1.5 | ? | 0.5–1.3 | 2–2.9 | 0.6–1.4 | 2–3.1 |
| Perianth lobe breadth (mm) | 0.4–0.8 | 0.5–0.9 | 0.7–1.5 | ? | 0.5–0.9 | 1.8–3.4 | 0.5–0.8 | 1–2 |
| Perianth lobe tip | obtuse | acute | acute | ? | acute | acute | acute | acute |
| Fruit elaiosome | present | short to absent | ? | ? | absent | absent | present | absent |
| Fruit colour | white | green | green | ? | green | white | green | golden–green |
| Fruit shape | truncate | ovoid | ovoid | ovoid | ovoid | ovoid | ovoid | globose |
| Fruit ribs | 5–ribbed | 10–ribbed | 10–ribbed | ? | 10–ribbed | ribs absent | 10–ribbed | ribs absent |
| Fruit length (mm) | 2–3.4 | 1.5–3 | 2–3 | ? | 1.8–2.5 | 2–3.2 | 1.3–2.8 | 1.5–3 |
| Fruit diameter (mm) | 1.8–2.7 | 1.2–2.5 | 2–2.5 | ? | 1.6–2 | 1–2 | 1–3.2 | 1–2.24 |
| Persistent perianth lobe colour | orange | green | green | ? | green | ? | green | golden–green |
| Substrate | sand dune | sandstone | sandstone/deep sand | ? | sandstone | shale and sandstone | sandstone/deep sand | quartz–silcrete |

### 3.3.5 Ultrastructural traits

The epidermal cells and pollen grains of species in subgenus *Hagnothesium* show diverse ultrastructure, as illustrated in Fig. 3.4. In *T. fragile* and allies, the species exhibit a range of stomatal types on stems, leaves and sometimes on perianth lobes. For example, on stem surfaces, *T. fragile* and *T. quartzicolum* possess anomocytic (five or more unequal-sized subsidiary cells, Fig. 3.4A) and tetracytic (four unequal-sized subsidiary cells around stomata, Fig. 3.4B) stomata respectively, while *T. microcarpum* have paracytic (two parallel subsidiary cells around stomata, Fig. 3.4C) complex types. Conversely, the leaves in species such as *T. hirtum* consistently have paracytic stomatal complex types (Fig. 3.4 D–E). The stomata are mostly perpendicular to the orientation of the subsidiary cells on leaves and stems (Fig. 3.4C–E). The epidermal cells and the subsidiary cells are almost the same shape, somewhat rectangular to polygonal, although narrower in depressed stipe areas or in ridges of the leaf or stem surfaces (Fig 3.4E). The anticlinal walls of epidermal cells are straight in all species, except in *T. microcarpum* in which cells are curved and randomly distributed (Fig. 3.4B–C). Paracytic stomata on the upper surfaces of perianth lobe segments of *T. microcarpum, T. fruticulosum, T. fragile* and *T. quartzicolum* (Fig. 3.4F) are diagnostic in these species but absent in *T. minus* (Fig. 3.4G), *T. longicaule* (Fig. 3.4H) and *T. hirtum* (Fig. 3.4I). However, irregularities in the anticlinal walls of the epidermal cells on the perianth lobe epidermis exist amongst species, ranging from wavy (Fig. 3.4G) to rectangular (Fig. 3.4H) to irregular in shape (Fig. 3.4I).

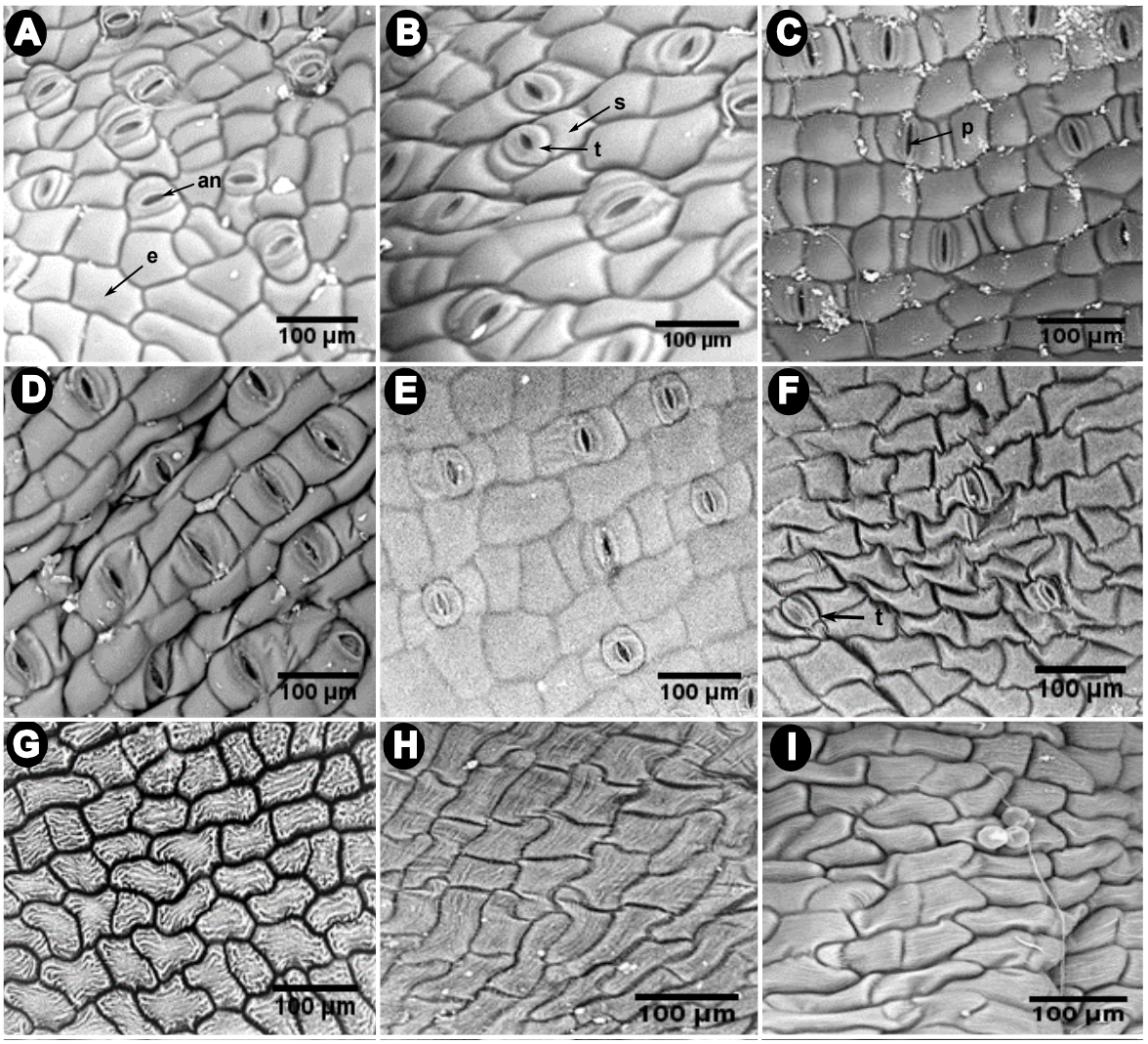



**Fig. 3.4:** SEM ultrastructural traits of species in the subgenus *Hagnothesium*. Stomatal complex traits of: A. *T. fragile*, (B) *T. quartzicolum*, (C) *T. microcarpum*, (D) *T. fruticulosum*, (E) *T. longicaule*, (F–I) portions of the upper surface of perianth lobe epidermis of *T. quartzicolum*, *T. minus*, *T. longicaule* and *T. hirtum*.

### 3.3.5 Ecological range

Members of the subgenus *Hagnothesium* are narrow-endemics of the GCFR, found mainly in the Fynbos and Renosterveld vegetation (Fig. 3.5). Within the GCFR, the occurrence of local endemic species provides useful taxonomic and geographical information for the group. For instance, *T. leptostachyum* is known only from the Karatara River area in the Knysna Division and *T. quartzicolum* is confined to the quartz-silcrete outcrop patches of the Overberg in the Bredasdorp Division. More widespread species across the GCFR include *T. microcarpum*, *T. fruticulosum* and *T. hirtum*. *T. minus* is also widespread, and has been collected from the mountain Fynbos areas of Caledon and Bredasdorp in the southwest, Riversdale in Langeberg and towards Port Elizabeth in the Eastern Cape (Fig. 3.5).

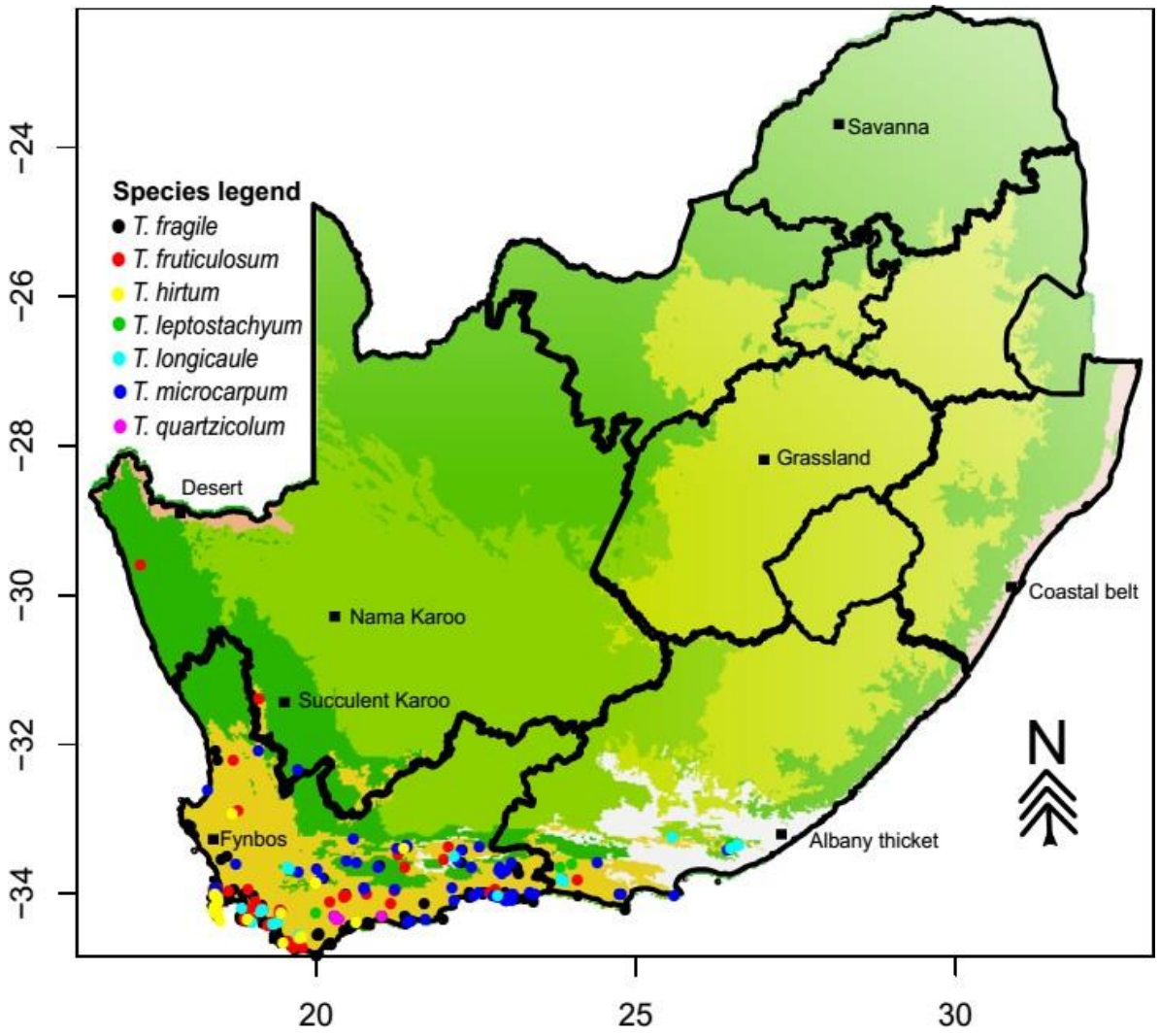



**Fig. 3.5:** Documented geographic range of *Thesium* species in subgenus *Hagnothesium*, showing species distribution endemic to the GCFR Fynbos Biome.

Substrate (Table 3.1) and elevation preferences also aid in the diagnosis of species within the subgenus *Hagnothesium*. For example, while *T. fruticulosum* and *T. longicaule* are consistently found on sandstone mountain slopes at elevations between 100–500 m above sea level (a.s.l.), *T. fragile* mostly occurs along the coastal belt on deep sands (sand dunes or coastal mountain slopes) from sea level to less than 100 m elevation. *Thesium microcarpum*, on the other hand, occurs on shale, deep sand or well-drained, sandy soil at elevations up to about 1500 m, and *T. quartzicolum* is endemic to quartz-silcrete soils between 200–300 m above sea level.

### 3.3.6 Multivariate analyses

The first three PCoA (49.1%, 16.6% and 11.5%, respectively) axes explained 77.2% of the variance in the morphological data (Fig. 3.6). The traits with the greatest contribution to this variation (in decreasing order of importance according to PCA Eigen vectors) plant height, male and female bract length, bracteole length, male and female leaf length and internode length. Based on the PCoA and PCA plots (Fig. 3.6; Appendix Fig. S3.1), it was possible to distinguish five clusters corresponding to species, namely: *T. quartzicolum, T. longicaule*, *T. minus, T. hirtum* and *T. fruticulosum.* These discrete clusters were recognized as distinct species. The specimens of *T. longicaule* clustered close to those of *T. fruticulosum* in both PCoA (Fig. 3.6) and the PCA phenogram (Appendix Fig. S3.2), and both showed overlap in most of the characters studied (Fig. 3.3). However, they differed in the lengths of their internodes (on both male and female plants), stem elongation and in leaf morphology (leaves acicular, convex and sparse in *T. longicaule*; leaves linear-lanceolate, concave, dense and imbricate in *T. fruticulosum*). The specimens of *T. longicaule* clustered close to those of *T. fruticulosum* in both PCoA (Fig. 3.6) and the PCA phenogram (Appendix Fig. S3.2), and both showed overlap in most of the characters studied (Fig. 3.3). However, they differed in the lengths of their internodes (on both male and female plants), stem elongation and in leaf morphology (leaves acicular, convex and sparse in *T. longicaule*; leaves linear-lanceolate, concave, dense and imbricate in *T. fruticulosum.* There was overlap between “species” pairs of *T. microcarpum* and that of *T. exocarpaeoides*. Furthermore, the specimen pairs of *T. thunbergii* and *T. fragile* formed a cluster (Fig. 3.6).

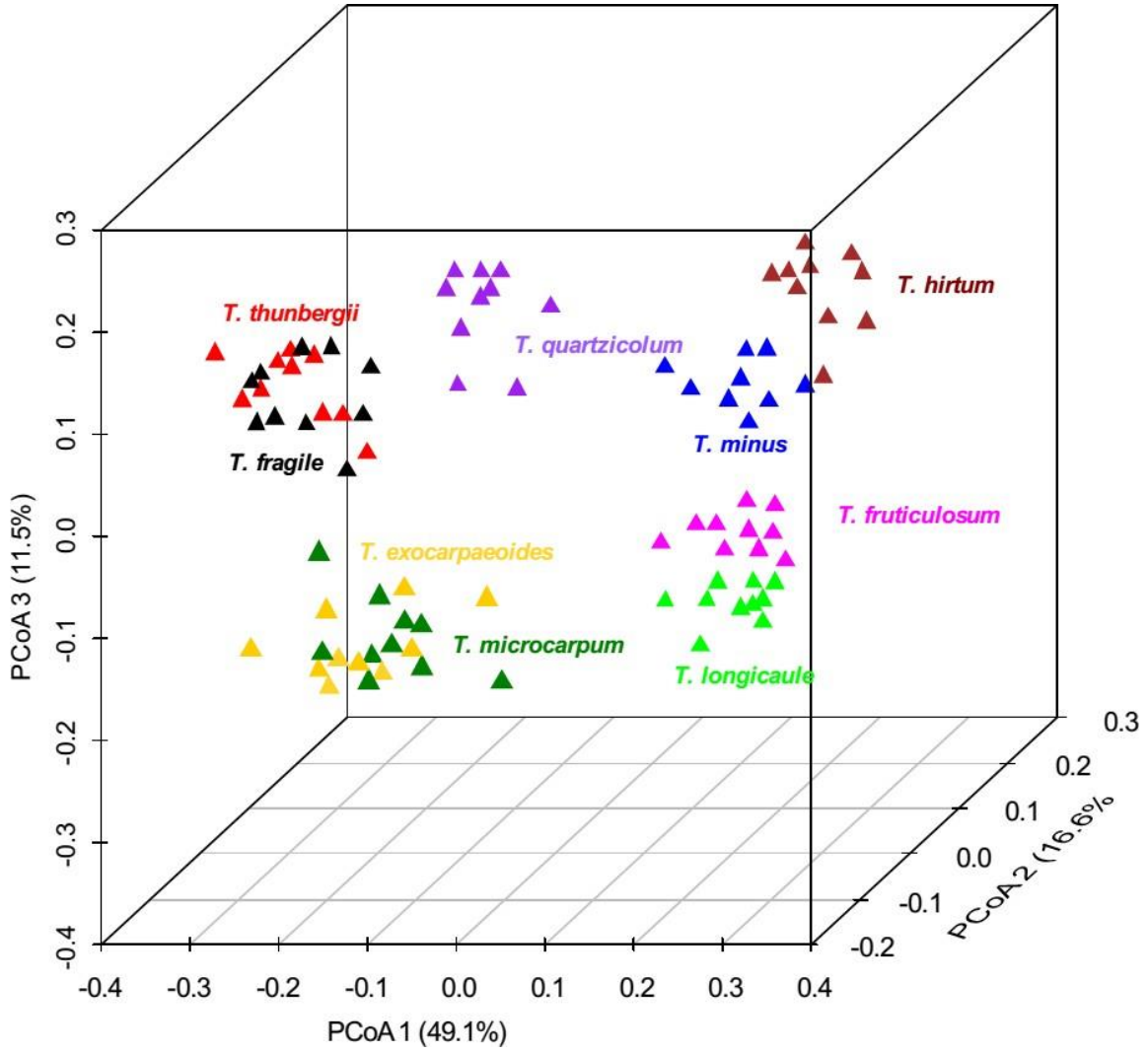



**Fig. 3.6:** Principal coordinate analysis based on 49 discrete and continuous characters of 90 *Thesium* specimens plotted on the first three principal coordinates.

### 3.4 DISCUSSION

The objective of this chapter is to assess whether the propensity of "splitting" a single species into several taxa or a case of the "lumping scenario" of several species into a distinct taxon exist within the subgenus *Hagnothesium.* Following Sneath's (1976) and Stace's (1989) "phenetic species" concept, we recognised each phenetic cluster as a distinct species. The phenetic criteria checks for morphologically coherent entities, and then a search for discontinuously-varying characters to test their evolutionary distinctness (de Queiroz, 2007). To support this approach, we re-evaluated the unifying morphological traits to each cluster (Nixon and Wheeler, 1990). In a sense, "the unified species concept" that equates species as a lineage which is evolutionarily isolated from other lineages, diagnosable using two or morphological traits (de Queiroz, 2007) was adopted.

The use of multivariate analyses for species delimitations has been propagated by several

authors (*e.g.*, Small and Brookes, 1990; Sebola and Balkwill, 2013; Koutecký, 2015). In addition, although geographical range cannot be used in isolation to delimit species, it has been used to support the phenetic clusters, that each recognisable cluster occupy a definable geographical area (Stace, 1989) and share the same ecological niche or adoptive zone (Andersson, 1990). Together, these lines of evidence were used to delineate each species.

Morphologically, it was difficult to assign male plants to the appropriate female plants of the same species in *T. fragile* and allies based on their vegetative traits (Hill, 1915b; D.A. Zhigila pers. obs.). This observation echoes the difficulties experienced by De Candolle (1857a), who described a single species (*T. strigulosum*) as two distinct species (*T. strigulosum* and *T. globosum*) from male and female plants, respectively (Hill, 1925). The complex vegetative similarities observed in species agree with Hill (1915b), who suggested that species in the then recognized genus *Thesidium* were diagnosable on vegetative traits, particularly leaves, bracts and bracteoles, rather than on geographical or reproductive traits. We found the internode to be an important taxonomic character, but it received limited attention in previous studies (*e.g.* Hill, 1915a; 1925). In this study, it was explored in detail and found to be useful for discriminating species in the subgenus *Hagnothesium*. For example, *T. longicaule, T. fragile,* and *T. quartzicolum* all have long internodes in both male (Fig. 3.3F; 3–13 mm) and female (Fig. 3.3E; 1.3–13.0 mm) plants. Conversely, *T. hirtum* and *T. fruticulosum* have short (0.5–4.0 mm) internodes in both male and female plants (Fig. 3.3F).

Although floral merosity and a dioecious breeding system are diagnostic traits of species in the subgenus *Hagnothesium* as a whole, the data suggest that floral traits have limited utility for discriminating species within the group. This accords with Hill's (1915b) observation of the similarity of floral characters in *Thesidium* and his suggestion that species within the group might be distinguishable exclusively on the basis of vegetative characters. There were, however, slight variations of floral characters, for instance, *T. quartzicolum*, *T. minus* and *T. microcarpum* have flowers from 2–5 mm long, whereas *T. fragile* and *T. fruticulosum* usually have flowers that are between 0.7 and 2 mm long.

The fruit in *T. fragile* and *T. microcarpum* are white, with a swollen elaiosome suggestive of dispersal by ants. Whereas, in *T. quartzicolum*, *T. hirtum* and *T. longicaule* the fruits are golden green with or without elaisome (Hill, 1925; Nickrent and García, 2015).

The ultrastructure of epidermal cells of members of subgenus *Hagnothesium* has never been studied before (*e.g.* in Hill 1915a, 1915b, 1925). According to Pilger (1935) species in Santalaceae are characterised by paracytic stomata, in which each guard cell is surrounded by a pair of parallel subsidiary cells. Here, they are shown to provide additional taxonomic support

for species delimitation (Fig. 3.4). For example, *T. microcarpum* differs from its affinities in having paracytic stomata (versus anomocytic and tetracytic type in *T. fragile* and *T. quartzicolum*).

Based on the PCoA and PCA analyses, the vegetative traits contributed more to species delimitation than reproductive traits (Appendix Table S3.2). These findings concur with the observations of Hill (1915b), who stated that species in *Thesidium* were separated almost entirely on vegetative traits of the leaves, bracts and bracteoles. In this study, we identified discrete clusters as distinct species, which conforms to the "phenetic species concept", which defines a species as cluster of taxa with certain similar morphological traits diagnostic to them (Stace, 1989; Ridley, 1993; Aldhebiani, 2018). Although each of the distinct clusters can be recognized based on one or few morphological traits, the phenetic breaks between species concur with the phylogenetic patterns (Moore et al., 2010), geographical ranges and spectra of dissimilarity displayed by members of each group (Fig. 3.6). The exceptions were *T. fragile* and specimens stored under the name *Thesidium thunbergii* which tightly resolved in the same cluster, supporting the suggestion to reduce *Thesidium thunbergii* to a synonym for *T. fragile* (Forest and Manning, 2013). Similarly, *T. microcarpum* and *Thesidium exocarpaeoides* cluster together to such an extent that it supports the latter to be a synonym to the former (Forest and Manning, 2013). Although *T. podocarpum* and *T. confusum* J.C.Manning & F.Forest are viewed as synonyms of *T. fragile* (Forest and Manning, 2013), they could unfortunately not be included in the multivariate analyses due to paucity of available specimens; only four vouchers were seen for *T. podocarpum* and none for *T. confusum.*

Although several characters unite *T. longicaule* to *T. fruticulosum*, they are separable based on the length of internodes, and stem and leaf characters (Table 3.1). On the other hand, the PCA plot (Fig.3.6) does not clearly separate the accessions into distinct species. Based on these, it was concluded that they are not conspecific. Hill (1915; 1925) described *Thesidium fruticulosum* and *Thesidium longifolium* as distinct species based on the striking difference in stem elongation, a major character differentiating them. However, Forest and Manning (2013) reduced *Thesidium longifolium* to a synonym of *Thesium fruticulosum.* Their decision was influenced by Levyns (1950), who had identified the former as a shade form of the latter. Her conclusion was not adopted here, as close morphological examination of the type specimens and other collections stored under these names provided sufficient trait differences to separate these two taxa.

We therefore propose that *Thesidium longifolium* be reinstated as a good species as *Thesium longicaule*. As the specific epithet *longifolium* is not available because the Eurasian

taxon (*Thesium longifolium* Turczaninow, in Bull. Soc. Imp. Nat. Moscou. 25: 469. 1852), was validly published under this name (Shenzhen Code: Turland et al., 2018). We therefore propose the name *T. longicaule* as an explicit substitute for the African *Thesidium longifolium.* Also, *Thesidium strigulosum* (A.DC in Esp. Nouv. 673: 1857b) was formerly called *T. hirtum* (Sonder in Flora 365: 1857a), but Forest and Manning (2013) rightly considered *Thesidium strigulosum* as an illegitimate name based on priority principle and adopted *Thesium strigulosum* as a new combination for this species. Unbeknownst to them, however, an Angolan taxon has been described as *Thesium strigulosum* (Welw. ex Hiern. in Fl. of Trop. Afr. 6(1). 411: 1913), which renders *T. strigulosum* an illegitimate name for the GCFR species under review here (Article 6, Shenzhen Code: Turland et al., 2018). We therefore propose the reinstatement of *Thesidium hirtum* as a new combination for this taxon.

**Table 3.2:** History of classification treatments in *Thesium* subgenus *Hagnothesium* to reflect the previous and current taxonomic placements. = denotes heterotypic synonyms. Names in bold represents accepted taxa. Gen. = genus, subg. = subgenus and sect. = section.

| De Candolle (1857a) | Sonder (1857b) | Hill (1915b, 1925) | Forest & Manning (2013) | Zhigila et al. (2020) |
|---|---|---|---|---|
| gen. *Thesium* | gen. *Thesidium* | gen. *Thesidium* | gen. *Thesium* | **gen. *Thesium*** |
| sect. *Hagnothesium* | | | sect. *Hagnothesium* | **subg. *Hagnothesium*** |
| *T. fragile* | *T. fragile* | *T. fragile* | = *T. fragile* | ***T. fragile*** |
| *T. podocarpum* | *T. thunbergii* | *T. thunbergii* | *T. confusum* | = *T. confusum* |
| *T. exocarpaeoides* | *T. exocarpaeoides* | *T. exocarpaeoides* | = *T. microcarpum* | ***T. microcarpum*** |
| | | | | ***T. quartzicolum*** |
| | | *T. fruticulosum* | = *T. fruticulosum* | ***T. fruticulosum*** |
| *T. strigulosum* | = *T. hirtum* | *T. hirtum* | = *T. strigulosum* | ***T. hirtum*** |
| *T. globosum* | | | | = *T. strigulosum* |
| | | *T. leptostachyum* | = *T. leptostachyum* | ***T. leptostachyum*** |
| | | *T. longifolium* | = *T. longifolium* | ***T. longicaule*** |
| | | | | = *T. longifolium* |
| | | *T. minus* | = *T. minus* | ***T. minus*** |

### 3.5 Conclusions

The total evidence approach supports the inclusion of *T. podocarpum, Thesidium thunbergii* and *T. confusum* as synonyms of *T. fragile* and *Thesidium exocarpaeoides* as a synonym of *T. microcarpum* (Hill, 1925; Forest and Manning, 2013; Table 3.2). Consequently, the data support treating *Thesidium longifolium* as a species and not a variety, but we propose the name *T. longicaule* (*nom. nov*.) as a replacement for taxonomic reasons. Also, *Thesidium hirtum* was reinstated for *T. strigulosum*, but as the new combination *Thesium hirtum*, as the epithet *strigulosum* has already been applied to another *Thesium* species (Table 3.2). We further identified *T. quartzicolum* as a new species that is similar to *T. fragile*, but it is distinguished by its terete stems, green fruits, yellowish green persistent perianth remnants and its preference for quartz-silcrete soil patches (versus *T. fragile*

with sulcate stems, white fruits capped with green, yellow to orange perianth remnants and preference for well-drained sandy soils, beach sand or coastal sand dunes). Ultimately, our observations agree with Hill (1925) that *T. leptostachyum*, excluded from the multivariate analyses, should be left undisturbed and was treated as *incertae sedis* as all effort to get more material from its known distribution regions proved abortive and only male specimens were available in herbaria.

### 3.6 Taxonomic treatments

#### 3.6.1. Key to the species in *Thesium* subgenus *Hagnothesium*

1a Male and female plants similar, leaves subrotund, triangular or ovate, bracts and bracteoles scale-like, bracts shorter than flower… .....2

1b. Male and female plants dissimilar, leaves adpressed, linear or lanceolate, seldom acicular, bracts and bracteoles leaf-like, bracts longer than flower…..... 4

2a. Plant sprawling, much-branched at distal portion, inflorescences crowded, fruit ovoid, substrate shale and sandstone……..…**3.6.3.5. *T. microcarpum***

2b. Plant erect, sparsely branched at basal portion, inflorescences lax, fruit globose or truncated, substrate quartz-silcrete, coastal sand or deep sand.....3

3a. Stem sulcate in transverse section, fruit white when mature, elaiosome present, persistent perianth segments longer than or equal to fruit, green when young, but turns yellowish then orange at maturity, substrate sand dune or coastal beach sand……..……**3.6.3.1. *T. fragile***

3b. Stem terete in transverse section, fruit green when mature, elaiosome absent, persistent perianth segments shorter than fruit, green when young and mature, substrate quart-silcrete ……..……..……**3.6.3.7. *T. quartzicolum***

4a. Plant scabrid on all vegetative parts, midrib with hispid structures on leaves, bracts and bracteoles, perianth lobe 1–2 mm long ……**3.6.3.3. *T. hirtum***

4b. Plant scabrid at leaf margins only, midrib without hispid structures on leaves, bracts and bracteoles, perianth lobe 0.5–1 mm long .....5

5a. Plant annual, 5–10 cm tall, rhizome present. ……..……...**3.6.3.6. *T. minus***

5b. Plant perennial, 15–30 cm tall, rhizome absent .....6

6a. Stem sulcate with verrucose edges, bracts and bracteoles with ciliated margins, perianth lobe segments distinctly uncinate, lobe margins scabrid……..……..**3.6.4.2. *T. leptostachyum***

6b. Stem sulcate with glabrous or hispid edges, bracts and bracteoles with entire margins, perianth lobe segments not uncinate, lobe margins entire .....7

7a. Leaves linear-lanceolate in male plants, leaf margins not cartilaginous, internode length 0.5–4 mm, midrib not raised, without hispid structures.…… **3.6.3.2. *T. fruticulosum***

7b. Leaves acicular in male plants, leaf margins cartilaginous, internode length 1–10 mm, midrib raised, with short hispid structures……..…**3.6.3.4. *T. longicaule***

**3.6.2** ***Thesium*** L. subgenus ***Hagnothesium*** (A.DC.) Zhigila, Verboom & Muasya ≡ ***Thesium*** sect. ***Hagnothesium*** A.DC. in Esp. Nouv. *Thesium*: 4 (1857). Type: *Thesium fragile* L.f. Lectotype designated by F.Forest & Manning 43(2): 215 (2013).

*Diagnosis.* – Plant dioecious, male and female plants similar like in *T. fragile* and allies or dissimilar like in *T. hirtum* and allies, plants brittle like in *T. fragile* or not brittle like in *T. hirtum* and allies, leaves linear or lanceolate to acicular like in *T. hirtum* and allies or scale-like like in *T. fragile* and allies, bracts and bracteoles leaf-like, bract shape triangular, linear or lanceolate, seldom acicular, longer relative to flower as in *T. hirtum* and allies or shorter as in *T. fragile* and allies; inflorescences in branchlets or leaf axils, solitary spikes, or borne in 2– 3-flowered dichasia, rarely solitary, flowers generally 4-merous, perianth lobe inner and outside colour green; fruit surfaces 10-ribbed, 5-ribbed or without ribs, reticulate veins conspicuous or faint, except in *T. microcarpum* and *T. quartzicolum*, in which veins are absent, ovoid to globose or truncated, fruit colour green or white, persistent perianth segments green when young, white or yellow to orange in mature plants, shorter or equal to fruit length.

### 3.6.3 Species descriptions and distributions in the subgenus *Hagnothesium*

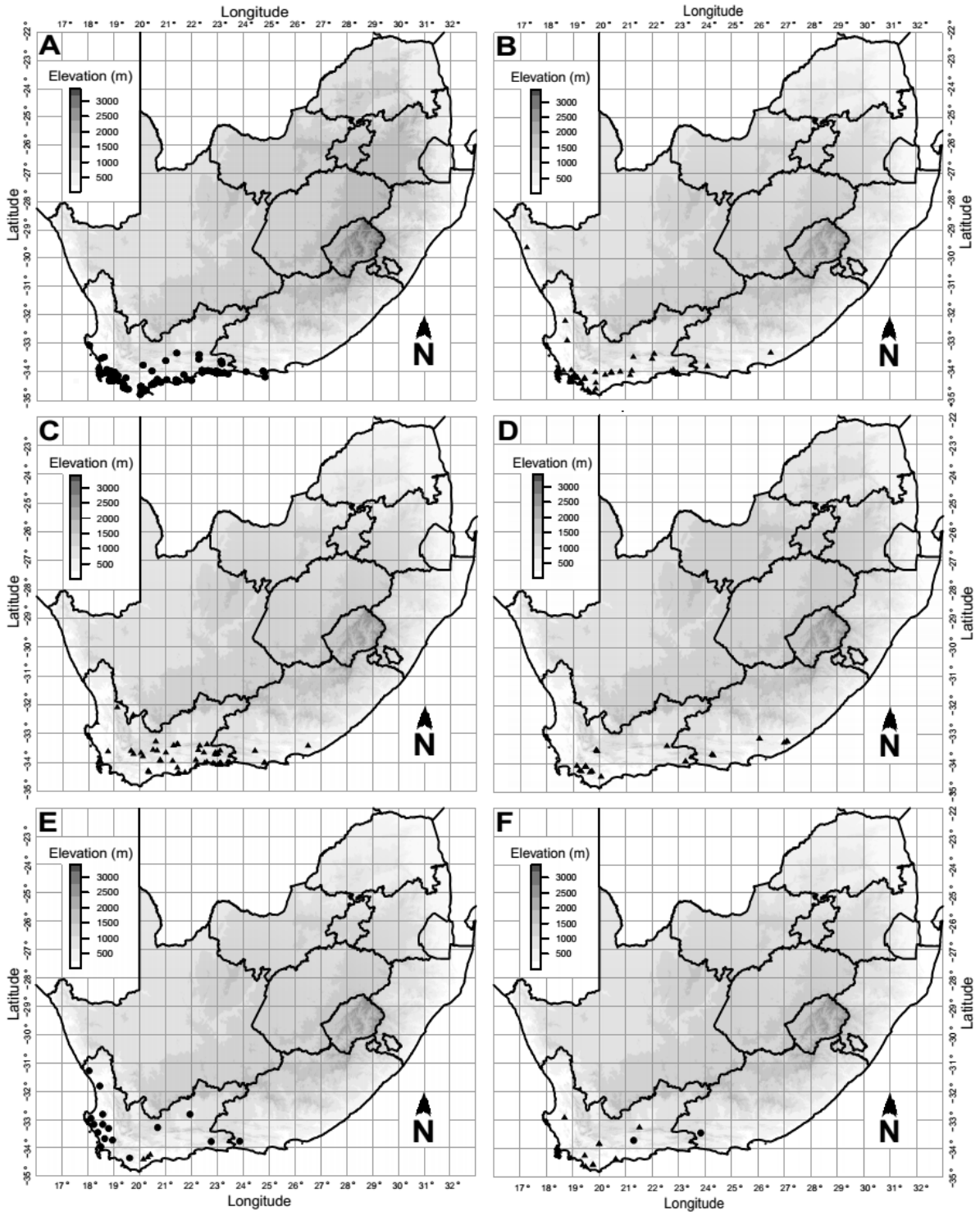



**Fig. 3.7:** Distribution of species of *Thesium* subgenus *Hagnothesium*: (A) *T. fragile*, (B) *T. fruticulosum*, (C) *T. microcarpum*, (D) *T. minus*, (E). *T. hirtum*, solid circle, *T. quartzicolum*, solid triangle, (F) *T. leptostachyum*, solid circle, *T. longicaule*, solid triangle.

**3.6.1.1.** ***Thesium fragile*** L.f. in Supplementarum Plantarum, 162 (1782).

≡ *Thesidium fragile* Sond. in Flora, 364 (1857a); A.W.Hill in Bull. Misc. Inform. Kew 3: 98 (1915); A.W.Hill in Fl. Cap. 5(2): 202 (1925). *Thesidium podocarpum* A.DC. in Esp. Nouv. Thesium: 5 (1857a); A.DC. in Flora, 674 (1857b). *Thesidium thunbergii* Sond. in Flora, 364 (1857a). Type: South Africa, Western Cape, Malmesbury Division, sand dunes at Saldanha Bay, ♂ & ♀ plants, date not precise, Ecklon & Zeyher 29 (K! Lectotype designated here, BOL!, FHO!, NBG!, OXF!, PRE!, Isolectotypes). *Ecklon & Zeyher 29* was selected as lectotype as it was cited in the protologue, deposited at Kew Herbarium together with other earlier collections of *Thesium* and signed by A.W. Hill who studied the material in depth.

An erect brittle suffrutex, 10–40 cm tall, heath-like, yellowish to golden green in appearance, with a woody rootsock and simple taproot, scarcely to much-branched, about 4–10 branches, branching pattern virgate, leaves subtending branchlet present or absent , if present then only at early growth stage. *Stems* woody at base, herbaceous at distal portion, 2–4 mm in diameter, erect, glabrous, sulcate or subangled in transverse section. *Leaves* sparingly distributed and almost reduced to scales, subrotund, adpressed to the stem, golden to yellowish green, glabrous, no prominent venation or midrib, leaf apex subacute to obtuse, margins entire or cartilaginous, recurved or straight. *Inflorescences* arranged along the branch length, in axils of branchlets, solitary, sessile; bracts and bracteoles reduced to scales, bracts fleshy, 0.7–1.5 × 0.5–1.3 mm, broadly triangular, margin slightly fringed with brown, membranous or cartilaginous edges, obtuse at tips, much shorter relative than flowers, incurved; bracteoles bract-like, but smaller, 0.5–1.2 × 0.4–1 mm; flowers campanulate, golden to yellowish green, 0.8–1.8 × 0.7–1.3 mm, 4-merous, rarely 5-merous, external gland absent between perianth lobes, perianth lobe segments 0.5–1.1 × 0.4–0.8 mm, ovate, obtuse at tips; hypanthium tube conspicuous, 0.3–0.5 mm long. Male and female plants similar. *Male plant:* branches robust and sparingly arranged along the stem length, internode 8–12.5 mm long; leaves lax, not imbricate, broadly ovate to triangular, 1–2.5 × 0.5–1 mm; inflorescence lax; hypanthium tube short to non-existent, shorter than perianth lobes, stamens four, rarely five; staminal filaments exserted at junction of hypanthium and perianth lobes, about 0.2 mm long. *Female plants:* branches robust, internodes 2–12.9 mm; leaves lax, not imbricate, broadly ovate to triangular, 1–2.2 × 0.5–1 mm; inflorescences spikes; hypanthium tubes more conspicuous, but shorter than perianth lobes; style stout, 0.3–0.5 mm long. *Fruit* nutlets, truncated to globose, white, attached to the branch by a truncated creamy elaiosome, 2–3.5 × 1.8–2.7 mm, with 5 conspicuous or faint ribs, with or without faint reticulation between the ribs, perianth lobe remnants persistent, green when

young, but turning yellow to orange with age, equal or shorter than fruit length (Fig. 3.8).

*Diagnostic characters.* – *Thesium fragile* is similar to *T. microcarpum* and *T. quartzicolum* but is best compared with the latter in its virgate growth form, brittleness, with male and female plants difficult to differentiate, sparse branching, branchlets jointed at node, leaves almost absent and reduced to scales, and inflorescences lax in both male and female plants and distributed along the branch lengths. It differs from *T. quartzicolum* in its perennial suffrutex habit, up to 40 cm tall, (versus herbaceous annual, up to ca 15 cm tall), robust rhizome, (versus slender rhizome), stem transverse section sulcate (versus terete), fruits truncated to globose, attached to the stem by a white elaiosome, capped with green or yellow to orange (depending on age) persistent perianth segments (versus fruits ovoid to subglobose, elaiosome absent, green to golden green, capped with green persistent perianth segments,), usually found on coastal well-drained sandy soil or sand dunes (versus confined to quartz-silcrete outcrops). It differs from *T. microcarpum* in branching pattern being sparse along the entire plant (versus dense at the upper part of plant in *T. microcarpum*), inflorescences lax (versus dense) and found on coastal beach sand (versus *T. microcarpum* found on sandstones and shale).

*Distribution and habitat.* – *Thesium fragile* occurs mostly along the coastal belt of the GCFR and is endemic to the region. It is restricted to sand dunes and well-drained beach sand from sea level to about 500 m above sea level in lowland Fynbos vegetation. It has been collected along the coastal hill slopes, beach sand flats and sand dune belts of the GCFR (Fig. 3.7A).

*Conservation status.* – Von Staden (2015) assessed *T. fragile* as a data deficient taxon and considered it as taxonomically problematic, probably as the species was poorly known and can easily be confused with *T. confusum* (Forest and Manning, 2013) or *T. microcarpum*. In our assessment, *T. fragile* is locally abundant in its major habitats and is found in most of the protected coastal reserves with no potential current threat. Although it is narrowly endemic to the coastal belts of the GCFR, we assess it as least concern (LC) under the IUCN Standards and Petitions Subcommittee (2017) guidelines.

*Additional specimens examined.* – South Africa. EASTERN CAPE: **3424 (Humansdorp):** without precise locality (-AA), 29 Mar 1918, ♀ plant, *Pillans 3938* (BOL); Palmietvlei (-BB), 09 Aug 1941, ♀ plant, *Parker 3577* (BOL); Coastal slopes, Witte Els Bosch (-BD), 01 Dec 1925, ♀ plant, *Fourcade 3168* (BOL); Uyshoek (-AB), 15 Mar 1977, ♂ & ♀ plants, *Thompson 3420* (PRE); Wilderness dunes (-BB), 03 Dec 1951, *Compton 23071* (BOL, NBG); Seal Point Nature Reserve, Cape St. Francis (-BB), 03 Nov 2004, ♂ & ♀ plants, *Forest, Trinder-Smith & Cowling 736* (NBG).

WESTERN CAPE. **3318 (Cape Town**): Oosterval, Langebaan (-AA), 24 Jul 1971,

*Axelson 459* (NBG). **3322 (Oudtshoorn):** Kleinplaat, George District (-DB), Feb 1879, ♀ plants, *Bolus 4759* (PRE); Homtini Pass, George (-DD), Aug 1926, ♀ plants, *Muir 4466* (BOL). **3323 (Willowmore):** De Hoop, Buffelsfontein (-AC), 09 Aug 1984, ♂ & ♀ plants, *Van Wyk 1790* (STE). **3418 (Simonstown):** near mouth of Palmiet River, Kogelberg Nature Reserve, Kleinond (-AC), 24 Mar 2008, ♂ plant, *Verboom 1305* (BOL); Harold Porter Botanical Reserve, Betty's Bay (-BD), 24 Sep 1963, ♂ & ♀ plants, *Jopper 160* (NBG); Pringle Bay (-BD), 11 Sep 1969, ♂ & ♀ plants, *Boucher 616* (STE, NBG); Swartklip (-BA), 24 Feb 1972, ♂ & ♀ plants, *Taylor 8076* (NBG, STE); Walker's Bay, littoral dune (-AD), 21 Mar 1973, ♀ plants, *Taylor 8365* (NBG, STE); Hangklip, Rooi-Els (-BD), 11 Mar 1981, ♀ plants, *Parsons 54* (NBG, STE); Gansbaai, Uilkraals river mouth (-CB), 12 Mar 1981, ♀ plants, *Parsons 125* (NBG, STE); Dunes opposite Malkopsvlei, Betty's Bay (-BD), 17 Mar 1983, ♀ plants, *Van Wyk 1197* (NBG, STE). **3419 (Caledon):** Pearly Beach, (-BC), 10 Jun 1950, *Maguire 3* (NBG); West of Franskraal (- CB), 09 Apr 1979, ♀ plants, *Hugo 1703* (NBG, STE); De Kelders, Gansbaai (-CB), 10 Oct 1981, ♂ & ♀ plants, *Mauve & Hugo 132* (NBG, STE); De Kelders, Gansbaai, near Klipgat pump station, next to disused road to the sea (-AC), 24 Nov 1990, ♂ & ♀ plants, *Fellingham 1515* (STE, NBG); Roadside on the northern outskirts of Gansbaai (-CB), 19 Jun 1995, ♂ & ♀ plants, *Paterson-Jones 393* (NBG); Coastal slopes, Wille Els Bosch, (-CA), 01 Oct 1936, ♂ & ♀ plants, *Fourcade 5347* (STE); De Kelders, Northwest of Klipgat Pump Station (-CB), 14 Apr 1990, ♂ plants, *Fellingham 1453* (NBG, STE). **3420 (Bredasdorp):** Papkuilsfontein, Bredasdorp, (-CA), 11 Jan 1956, ♂ plants, *Rycroft 1834* (NBG); Pearly Beach, 10 Jun 1950, ♀ plants, *Maguire 30* (NBG); De Hoop Nature Reserve, Windhoek (-CB), 26 Dec 1946, ♀ plants, *Compton 18994* (STE); 3 miles from Arniston to Bredasdorp (-CA), 27 Jul 1970, ♂ & ♀ plants, *Merwe 104* (NBG, STE); Witsand river mouth (-BC), 06 Nov 1979, ♀ plants, *Hugo 1909* (NBG, STE); Agulhas, westward from the light house (-CC), 25 Mar 1982, ♂ & ♀ plants, *Fellingham 383* (NBG, STE); De Hoop Buffelsfontein (-CB), 09 Aug 1984, ♂ & ♀ plants, *Van Wyk 1784* (NBG, STE); De Hoop Buffelsfontein (-CB), 29 Apr 1985, ♂ & ♀ plants, *Fellingham 1017* (NBG, STE); Marloth Nature Reserve (-AD), 25 May, 1903, ♀ plants, *Pearson 14* (BOL, NBG); De Hoop Nature Reserve, Whale trail, near Koppie Alleen (-BC), 17 Oct 2004, ♂ plants, *Forest & Lucas 715* (NBG, STE). **3421 (Riversdale):** Still Bay, sand dune below rubbish dump, southerly aspect, steep slope, (-CC), 28 Dec 1978, ♂ & ♀ plants, *Bohnen 4903* (STE, NGB); ca 3 km on road from Vermaaklikheid to Puntjie (-BD), 29 May 1984, ♂ & ♀ plants, *Callaghan, Fellingham & van Wyk 424* (NBG, STE); Still Bay, near estuary, (-AD), 11 Jan 19, ♀ plant, *Bohnen 4961* (PRE); Still Bay, Botterkloof, at the road to Riversdale (-AD), 04 May 2006, *Mucina*

*040506/29* (NBG); Rubbish dumps, Still Bay (-AD), 10 Mar 1980, ♂ plants, *Bohnen 7433* (NBG, STE); road above Panorama circle (-AD), 18 Jul 1980, ♀ plant, *Bohnen 7585* (NBG, STE). **3422 (Mossel Bay):** Buffalo Bay, near Walker pond (-AA), 02 Feb 1936, ♀ plants, *Guthrie 5347* (BOL); Groot Brak river mouth (-AA), 13 Nov 1981, ♂ & ♀ plants, *Parsons 372* (NBG, STE). **3423 (Knysna):** Forest near Portland, Knysna (-AA), 01 Feb 1929, ♀ plants, *Duthie 1103* (STE); Buffalo Bay, near Knysna (-AA), 29 Apr 1969, ♂ & ♀ plants, *Barker 10608* (NBG); Robberg Nature Reserve (-AB), 29 May 1970, ♂ plants, *Taylor 7700a* (NBG, STE); Goukamma Nature Reserve (-AA), Feb 1970, ♀ plants, *Merwe 1736* (NBG, STE).

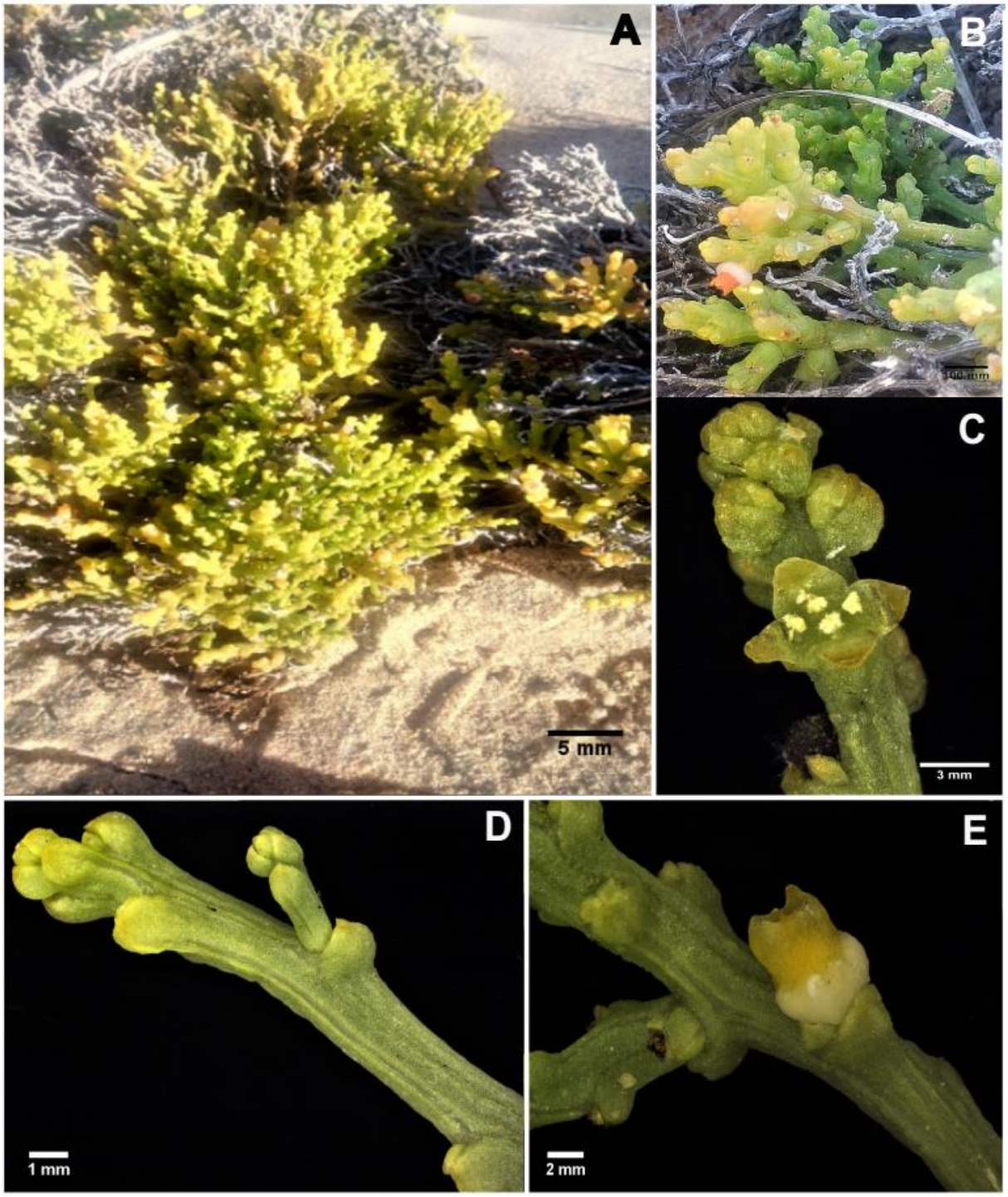



**Fig. 3.8:** *Thesium fragile*: (A) growth habit and coastal sand substrate of the plant, (B) closer view of a fruiting female plants, (C) flowering shoot showing four stamens, flower and stamens in male plant, (D) indeterminate flowering shoot with scale-like leaves subtending branchlets, bracts and bracteoles, (E) female shoot with truncate, whitish fruit capped with long, yellowish, persistent perianth remnants. Photographs: Daniel Zhigila.

**3.6.1.2. *Thesium fruticulosum*** (A.W.Hill) J.C.Manning & F.Forest in Bothalia 43(2): 215 (2013). ≡ *Thesidium fruticulosum* A.W.Hill in Bull. Misc. Inform. Kew 3: 98 (1915); A.W. Hill in Fl. Cap. 5(2): 205 (1925). Type: South Africa. Western Cape, Caledon (3420AB): Vogelgat, *Austro-Africanae. Regio occidentalis*. Vogelgat, 11 Apr 1897, *Schlechter 10414* ♂ and ♀ *10415* (L, lectotype, designated here; BOL!, HBG!, K!, NBG!, PRE! isolectotypes). The assignment of *Schlechter 10414* as lectotype is supported by its locality within the typical geographical range of the species and is one of the six specimens cited by Hill (1925), and it has both male and female plants on the same sheet.

An erect or spreading perennial suffrutex, up to about 30 cm tall, heath-like or growing beneath other shrubs, golden green in appearance, plant not brittle, woody taproot or slender rootstock, branched mainly from basal part, 5–15 branches, branching pattern fastigiate, leaves subtending each branchlet. *Stems* woody at base, herbaceous above, 2.0–3.5 mm in diameter, erect or suberect, glabrous to subglabrous, terete in transverse section. *Leaves* well-developed, erect to adpressed to the stem, green basally, but turning golden toward the attenuate tips, glabrous and glossy, without prominent venation or midrib, apex acute, margins entire, concavely recurved, rarely straight. *Inflorescences* arranged along the branch length, in spikes in branchlet axils, attached to the stem by a short or no pedicel; bracts and bracteoles leaf-like; bracts fleshy, 2–6 × 1–2 mm, linear-lanceolate, margins conspicuously ciliated, membranous, golden green, particularly toward the basal part, acute at tips, much longer than the flower, incurved; bracteoles bract-like, but smaller, 2–4 × 0.7–2 mm. Flowers campanulate, golden green, 1–2.5 × 0.8–1.5 mm, 4-merous, external gland between perianth lobes absent; perianth lobe segments 0.5–1.2 × 0.5–0.8 mm, lobes ovate to triangular, obtuse or subacute at tips, neither distinctly uncinate nor lobulate; tube ca. 0.5 mm long. Male and female plants well differentiated. *Male plant:* branches more slender than in female plant, internodes 0.5–4 mm long; leaves dense, almost imbricate, more slender than female leaves, linear-lanceolate, 3–6 × 0.5–1.5 mm; inflorescences lax; hypanthium tube shallow; stamens four, staminal filaments exserted at the junction of hypanthium and perianth lobes, about 0.3 mm long. *Female plant:* branches more robust, internodes as short as in the male plants, 0.5–3.6 mm; leaves dense, imbricate, linear, 10–11 × 1–1.5 mm. inflorescences lax; hypanthium tube shorter than the perianth lobes; style stout, about 0.3 mm long. *Fruit* a nutlet, ovoid, green, attached to the branch by white attenuated elaiosome, 1.5 –3 × 1–2.5 mm, with 10 conspicuous ribs, rarely 5, with prominent venation connecting the ridges, particularly when dry, capped with green persistent perianth lobe segments, shorter than the fruit (Fig. 3.11).

*Diagnostic characters.* – *T. fruticulosum* is similar to *T. minus* in having glabrous parts, terete stems, a fastigiate branching habit mainly from the base, linear leaves that are 3–10 cm long, a midrib that is not raised, and bracts and bracteoles that are leaf-like. *T. fruticulosum* differs in being a 15–30 cm tall, perennial suffrutex with a woody taproot system, without a rhizome (versus a 5–10 cm tall, annual herb with a fibrous perennial root system, and a rhizome), internodes 0.5– 3 mm in female plants (versus 3–8.5 mm), leaves in both male and female plants similar (versus leaves smaller in males than females) and fruits consistently with elaiosomes (versus fruit with or without elaiosomes).

*Distribution and habitat.* – Although *T. fruticulosum* has a widespread distribution, it is undercollected from Soebatsfontein to Brandberg in the Northern Cape, and from the coastal and mountain fynbos of the Western Cape eastwards to Grahamstown in the Eastern Cape (Fig. 3.7B). It occurs in mountain fynbos-renosterveld and the drier areas of Succulent Karoo favouring sandstone flats and mountain flanks, on rich or nutrient-poor rocky soil across the GCFR, from sea level to about 1500 m above sea level. It has been collected on coastal beach sands, deep sandy flats and sandstone mountain slopes across the southwest in the Western Cape to southeast in the Eastern Cape (Manning and Goldblatt, 2012). It also occurs in mountain fynbos, shale renosterveld and on gentle slopes of forest edges in the Kogelberg State Forest, Southern Hottentots Holland Mountains, Langeberg and the upper slopes of the Swartberg Mountains.

*Conservation status.* – Since *T. fruticulosum* is abundant across its geographical range, Von Staden (2015) assessed it as LC (least concern). Our data support this assessment.

*Additional specimens studied.* – South Africa. NORTHERN CAPE: **2917 (Namaqualand):** 4.7 km W of Komaggas-Soebatsfontein road to Brandberg (-CD), on well-drained sandy soil, 20 Oct 1986, ♂ & ♀ plants, *Le Roux & Lloyd 732* (STE). **3119 (Calvinia):** without precise locality, (-BC), 1969, ♂ & ♀ plants, *Heinecken 233* (BOL).
EASTERN CAPE: **3324 (Steytlerville):** St. Francis Bay (-BC), 02 Feb 1961, ♀ plants, *Levyns 11124* (BOL).

WESTERN CAPE: **3218 (Clanwilliam)**: 9.5 miles SW of Redelinghuys, Piketberg (-AD), 25 Aug 1958, *Acocks 19698* (PRE). **3318 (Cape Town):** Wynberg coastal hill slopes (-AB), 28 Nov 1897, ♂ & ♀ plants, *Galpin* 4556 (BOL). **3418 (Simonstown):** Dias beacon ridge, Simonstown, (-BD), 18 Dec 1965, *Taylor 6629* (STE); Cleared slope, Kirstenbosch (-AB), 26 Oct 1936, ♂ & ♀ plants, *Levyns 5908* (BOL); Southern Hottentots Holland Mountains, Kogelberg State Forest (-BD), 27 Oct 1992, ♀ plants, *Kruger 857* (NBG, STE). **3419 (Caledon):** Betty's Bay Nature Reserve (-AA), 01 Aug 1963, ♂ & ♀ plants, *Stauffer 5053*

(BOL); Along R321, 7.2 km NE of Grabouw and N2 (-AA), 15 Dec 2007, ♂ & ♀ plants, *García & Lopez 4058* (NBG); Vogelgat, above Dragonfly Pool (-AD), 01 Apr 1897, ♀plants, *Williams 3794* (BOL); Rietfontein Nature Reserve, western point of Soetanysberg (-DD), 23 Mar 1982, ♂ plants, *Van Wyk 806* (NBG, STE); North west Buffeljagtsberg (-DA), 11 Mar 1979, ♂ plants, *Thompson 3946* (NBG, STE); Fernskloof Nature Reserve, Hermanus (-AB), 24 Aug 2018, ♀ plants, *Zhigila 267* (BOL, K, NBG); ♂ & ♀ plants, *Zhigila 268* (BOL, K, NBG) . **3420 (Bredasdorp):** Hagel Kraal, limestone hill, (-BC), 28 Dec 1946, *Compton 19039* (NBG). **3422 (Mossel Bay)**: Goukamma National Reserve (-BB), without specific date, ♀ plants, *Heinecken 266* (BOL); Goukamma (-BB), 01 Dec 1971, ♂ & C, *Heinecken 267* (PRE); Hills S of Buffalo Bay (-CD), 01 Dec 1928, ♂ & ♀ plants, *Salter 318/3* (BOL).

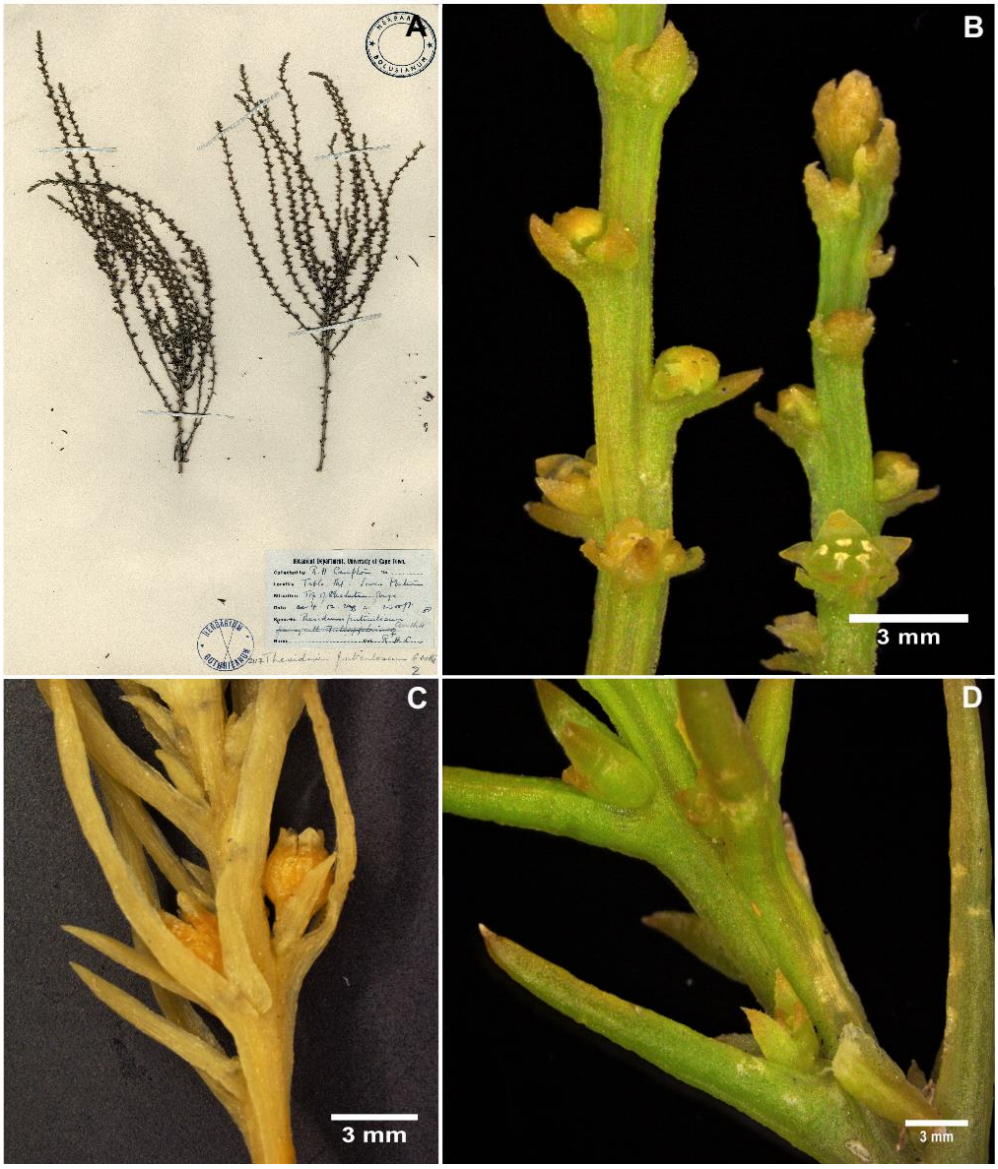



**Fig. 3.9:** *Thesium fruticulosum*: (A) Herbarium specimen of the male plant, (B) male flowering shoot showing 4-merous flower and stamens, (C) fruiting female plants with short internodes, dense leaves, bracts and bracteoles longer than fruit, (D) female plants showing flowering shoot, bract broken to display flower. Photographs: Daniel Zhigila.

**3.6.1.3. *Thesium hirtum*** (Sond.) Zhigila, Verboom & Muasya ***comb. nov.***

≡ *Thesidium hirtum* Sond. in Flora 40: 364 (1857a). *Thesium strigulosum* A.DC in DC. Prodr. 14: 673 (1857a). = *Thesidium strigulosum* (A.DC.) A.DC. based on female plants (in DC. Prodr. 14: 673 (1857b). Type: South Africa, Western Cape, Cape Town (3318): Table Mountain, near Constantia (-BD), without precise date, ♂ & ♀ plants, *Ecklon & Zeyher 35* (M, BOL, S syntypes).

*Thesium globosum* A.DC. in Esp. Nouv. Thesium 4: (1857a). *Thesidium globosum* (A.DC.) A.DC. based on male plants in DC. Prodr. 14: 673 (1857b). Type: South Africa, Western Cape, Cape Division, Table Mountain Nature Reserve (3418CD), Constantia neck, ♂ & ♀ plants, *Bolus 4689* (BOL, lectotype! designated here; K!, PRE! isolectotypes). We chose this lectotype as it contains both male and female plants and is cited by Hill (1925) as one of the syntypes.

An erect heath-like perennial suffrutex, 10– 5 cm tall, yellowish green in appearance, plant not brittle, taproot stout, branches arise mainly at basal portion, 3–12 branches, branching pattern fastigiate, leaves subtending branchlets. *Stems* woody at base, herbaceous above, 1–3.0 mm in diameter, erect or suberect, scabrous, conspicuously sulcate in transverse section, with hispid structures at edges. *Leaves* well-developed, incurved with tips adpressed to the stem, green at basal portion, but turn yellowish toward the attenuate tips, plant surface scabrid, raised midrib with short hispid protrusions, leaf apex acute, margins ciliate, sharp-edged, mostly straight, seldom concave. *Inflorescences* arranged in axils of branchlets along the branch length in short solitary or dense spikes, sessile or attached to the stem by a short pedicel; bracts and bracteoles leaf-like; bracts thick, 2–4 × 1.5–3 mm, ovate to lanceolate, conspicuously scabridulous on transparent margins, yellowish-green, acute at tips, longer than the flowers, usually curved; floral bracteoles bract-like, but smaller, 2–3 × 0.5–2.5 mm; flowers campanulate, yellowish green, 1–2 × 1–1.8 mm, 4-merous, external gland between perianth lobes absent, perianth lobe segments 0.5–1.5 × 0.5–1 mm, lobes ovate to lanceolate, obtuse or subacute at tips, neither distinctly uncinate nor lobulate; lobe tube short, about 0.2 mm. Male and female plants well differentiated. *Male plant*: branches more slender than in female plants, internodes short, 0.7–1.6 mm long; leaves dense, closely imbricate, male leaves as thick as female leaves, lanceolate, 2–3 × 0.5–1.5 mm; inflorescences lax; hypanthium tube short to non-existent, stamens four, staminal filaments attached to the walls of perianth lobe at base of tube, about 2.5 mm long, leaves dense, imbricate, linear to linear-lanceolate, 2.4–6 × 0.5–1.5 mm. *Female plant*: branches more woody than in male plants, internodes short, 0.7–1.5 mm long as in male plants; leaves dense, imbricate, linear-lanceolate, 6–12 × 0.5–2 mm; inflorescences

lax; hypanthium tube shorter than the perianth lobes, but longer than in male plants; style stout, 0.2–0.6 mm long. *Fruit* a nutlet, ovoid, pale green, elaiosome absent, 2–3 × 2–2.5 mm, with 10 conspicuous ribs, with reticulate venation in between ribs, capped with orange to golden green, persistent perianth segments that are shorter than the fruit (Fig. 3.12).

*Diagnostic traits. – T. hirtum* is similar to *T. fruticulosum* in its growth form, linear to lanceolate leaves, leaf-like bracts and bracteoles that are longer than flowers, inflorescences in bract axils subtended by tufts of bracteoles and ovoid fruits. *Thesium hirtum* is readily distinguished by its hirsute plant surface on the entire plant surface (versus glabrous), conspicuously keeled leaves, leaf margins erose and ciliate along the ridges of the midrib and leaf margin (versus leaves not keeled, midrib almost absent or subterete, without prominent ridges in *T. fruticulosum*).

*Distribution and habitat. – Thesium hirtum* is widespread across the lower slopes of the entire coastal mountain ranges of the West Coast Peninsula to Cape Peninsula to Potberg in the De Hoop Nature Reserve and toward the Groot Swartberg Nature Reserve in the Western Cape (Fig. 3.7E, solid circles). It has been collected in coastal Fynbos and on sandstone mountain Fynbos, but also rarely on quartz or limestone hills from sea level to c. 1300 m above sea level.

*Conservation status. – Thesium hirtum* has been designated as LC (Least Concerned) (Raimondo et al., 2009; Von Staden, 2015) as species are found in Nature Reserves across its range. Our assessment supports this status. However, with current stochastic events of recurrent fires in the Western Cape Province, plant populations with poor post-fire regeneration such as *T. hirtum* might be negatively impacted and threatened (Bond and Van Wilgen, 1996), and need to be monitored.

*Additional specimens studied.* – South Africa. WESTERN CAPE. **3218 (Clanwilliam)**: Lokenburg; 21 mi S of Nieuwoudtville (-CA), 25 Aug 1958, ♂ & ♀ plants, *Story 4348* (PRE). **3318 (Cape Town):** Table Mountain (-AB), Sep 1963, ♀ plants, *Stauffer 5141* (PRE); Wynberg hills, (-AB), 28 Aug 1963, ♀ plants, *Staufer 5053* (BOL). **3321 (Ladismith):** Berfontein, west hills of Witteberg, above Witelsrivier, Langeberg (-DC), 12 Nov 1931, ♀ plants, *Compton 3852* (BOL). **3322 (Oudtshoorn):** near Robinson (-DC), 26 Sep 1991, ♂ & ♀ plants, *Leighton 3157* (BOL). **3323 (Willowmore):** Donkerhoek se Nek, Prince Alfred's Pass (-DD), 16 Feb 1964, ♂ & ♀ plants, *Levyns 11508* (BOL). **3418 (Simonstown):** near Rainfall Exclusion Experiment Plots, Kalk Bay ridge, Steenberg (-AB), 10 Oct 2009, ♀ plants, *Moore 177* (BOL); Simons Bay, near Simons Town (-AC), ♂ & ♀ plants, *Zeyher 3815* (K, S); Hills near Simon's Town (-CA), 30 Jun 1918, ♂ & ♀ plants, *Bolus 3939* (BOL); Constantia neck, Table Mountain Nature Reserve (-CD), 01 Jan 1879, ♂ & ♀ plants, *Bolus 4689* (BOL); Smith's farm,

Cape Point, (-BD), 16 Jan 1936, ♂ & ♀ plants, *Compton 6047* (NBG); Table Mountain, near Constantia neck (-BD), without precise date, ♂ & ♀ plants, *Ecklon & Zeyher 35* (BOL); Silvermine (-AC), 04 Apr 2017, ♀ plants, *Zhigila 114* (BOL); N slopes, Constantiaberg (-AB), 29 Aug 1963, ♂ & ♀ plants, *Stauffer 5070* (BOL, PRE). **3419 (Caledon)**: Elim (-CD), 20 May 1996, ♀ plants, *Schlechter 7642* (BOL26299); hills in Rietfontein area, Elim, 01 Dec 1928, ♂ plants, *Bolus 318/4* (BOL); Zwartberg, 09 Dec 1896, *Bolus 8602* (BOL). **3420 (Bredasdorp):** Montibus, Koude River (-DA), 04 Dec 1896, ♂ & ♀ plants, *Schlechter 9627* (PRE); near Elim (-AD), 04 Dec 1898, ♂ & ♀ plants, *Schlechter 9628* (BOL); Limestone Hills, Pearly Beach (-AC), Without precise date, ♀ plants, *Esterhuysen 32996* (BOL); Upper flats above Boskloof, Potberg Mountain (-BC), 18 Aug 1980, ♂ plants, *Burgers 2440* (NBG, STE).


**Fig. 3.10:** *Thesium hirtum*: (A) habit based on *Esterhuysen 32996* (BOL), (B) a twig of a female plant, (C) a twig of a male plant, (D) lanceolate leaf with raised midrib and scabrid surfaces, (E) fruits. Photographs: Daniel Zhigila.

**3.6.1.4. *Thesium longicaule*** Zhigila, Verboom & Muasya ***nom. nov.***

Basionym: *Thesidium longifolium* A.W.Hill in Bull. Misc. Inform. Kew 3: 99 (1915).

≡ *Thesium longifolium* (A.W.Hill) J.C.Manning & F.Forest in Bothalia 43(2): 215 (2013); non *Thesium longifolium* Turcz. Published in: Bull. Soc. Imp. Natur. Moscou, 11: 100 (1838).

Type: South Africa. Western Cape, Cape Town (3318): Eastern side of Table Mountain (-AB), 365.8 m, July 1880, *Bolus 4608* (BOL! Holotype, HBG! K!, NBG!, PRE! Isolectotypes). *Bolus 4608* was designated as lectotype as it clearly shows the diagnostic characters and has female and male plants present on the same sheet.

A suberect or sprawling perennial suffrutex, 20–30 cm tall, heath-like or growing under other shrubs, green to yellowish green, brittle, particularly when dry, woody taproot with slender fibrous rootstock, branched mainly at base part, 3–15 branches, branching pattern fastigiate, leaves subtending each branchlet. *Stems* woody at base, herbaceous at distal portion, slender, 1.5–2.5 mm in diameter, sprawling or suberect, sub-hispidulous, conspicuously sulcate in transverse section. *Leaves* well-developed, incurved to adpressed to the stem, golden green, plant surface shortly hispid, without prominent venation, midrib conspicuously raised, leaf apex acute, margins membranous, straight, rarely convex or concavely recurved. *Inflorescences* arranged along the branch length, spikes in branchlet axils, attached to the stem by a short or no pedicel; bracts and bracteoles leaf-like; bracts not fleshy, 5–10 × 2–2.5 mm, linear to acicular, margins entire, cartilaginous or membranous, golden green, acute at tips, longer than the flower, concave or convex; bracteoles bract-like, but smaller, 3–4 × 0.4–2 mm; flowers campanulate, yellowish green, 2–3.7 × 0.8–1.5 mm, 4-merous, external gland between perianth lobes absent, perianth lobe segments 0.5–1.5 × 0.5–0.9 mm; lobes ovate to triangular, obtuse at tips, not distinctly uncinate, lobulate or straight, tubes inconspicuous. Male and female plants well differentiated. *Male plant*: branches more slender than in female plants, internodes 4–10 mm long; leaves fewer, more slender than female leaves, acicular, 5–10 × 0.4–0.8 mm; inflorescences lax; stamens four, staminal filaments exserted at junction of hypanthium and perianth tube, hypanthium shallow, about 0.2 mm long. *Female plant*: branches more robust, internode short compared to male plants, 1–5 mm long; leaves sparse, not imbricate, linear, 8–19 × 0.5–1.5 mm; inflorescences lax; hypanthium tube length shorter than the perianth lobes; style stout, between 0.2 and 0.4 mm long. *Fruit* a nutlet, subglobose, green, attached to the branch by a white attenuated elaiosome, 1.8–2.5 × 1.7–2 mm, with 10 conspicuous ribs and reticulate veins between ribs, capped with green persistent perianth lobe segments, shorter than the fruit (Fig. 3.13).

*Diagnostic characters.* – *Thesium longicaule* is easily confused with *T. fruticulosum* or *T. hirtum* as all three species have a fastigiate branching pattern, leaf-like bracts and bracteoles subtending inflorescences, flowers in spikes, and 10-ribbed fruits with conspicuous veins running between longitudinal ribs. *T. longicaule* differs from both by being more slender, particularly the male plants (versus robust), brittle (versus not brittle), with wider internodes, 4–10 mm long (versus internodes short to almost absent, 0.2–2 mm long), stems sulcate with ridge edges sub-hispidulous (versus glabrous in *T. fruticulosum* and scabrous in *T. hirtum*), and leaves sparse, linear or acicular, concave or convex (versus many, dense, almost overlapping, straight, rarely incurved in *T. fruticulosum* and *T. hirtum*).

*Distribution and habitat.* – *Thesium longicaule* occurs on sandstone in mountain Fynbos and on sandstone flats and slopes of the GCFR from the Cederberg to the Swartberg, mainly on rocky mountain slopes. It has been collected in the Olifants Sandstone Fynbos and Cederberg Sandstone Fynbos, North Outeniqua Sandstone Fynbos, South Outeniqua Sandstone Fynbos vegetation types (Fig. 3.7F, solid triangles) between elevations of 150 to 1200 m above sea level.

*Conservation status.* – With the distinction of *T. longicaule* from *T. fruticulosum*, the conservation status of *T. longicaule* is here assessed as LC (Least concern) as it is abundant over its local geographical range (IUCN Standards and Petitions Subcommittee, 2017).

*Additional specimens studied.* – South Africa. WESTERN CAPE: **3218 (Clanwilliam):** Olifants Rivier, (-DB), 03 Dec 1950, ♀ plants, *Esterhuysen 17862* (BOL). **3318 (Cape Town):** Table Mountain (-AB), Dec 1924, ♀ plants, *Compton 2117* (BOL); Oct 1940, ♀ plants, *Esterhuysen 23237* (BOL). **3321 (Ladismith):** García's Pass (-CC), 22 Mar 1938, ♀ plants, *Compton 8156* (BOL). **3322 (Oudtshoorn):** near Groeneweide Park (-CD), 03 Dec 1950, ♀ plants, *Esterhuysen 17863* (BOL). **3418 (Simonstown):** Near Muizenberg Reservoir (-CA), 22 Jan 1933, ♂ plant, *Salter 2954* (BOL); N of Window stream, Kirstenbosch (-AB), Jul 1880, ♂ & ♀ plants, *Bolus 4608* (BOL) Contour path near, Kirstenbosch, (-CC), no precise date, ♂ plant, *Compton 8187* (BOL); upper Kirstenbosch, near Diamond stream (-CD), 22 Mar 1938, ♂ & ♀ plants, *Compton 8157* (BOL). **3419 (Caledon):** Lebanon catchment II (-AA), 11 Nov 1967, ♂ & ♀ plants, *Kruger 562* (PRE); Hermanus (-AB), 21 Dec 1942, ♂ & ♀ plants, *Compton 14253* (NBG); Betty's Bay, 02 Feb 1961, ♂ & ♀ plants, *Levyns 11125* (BOL).


**Fig. 3.11:** *Thesium longicaule*: (A) habit and substrate of female plants, (B) habit of male plant based on *Bolus 4608* (K!), (C) male flowering shoot, (D) detailed male flowering shoot, (E) female fruiting shoot. Photographs: Daniel Zhigila.

**3.6.1.5.** ***Thesium microcarpum*** A.DC. in Esp. Nouv *Thesium*: 5 (1857a), *Thesidium microcarpum* A.DC. in Flora 674 (1857a). *Thesidium exocarpaeoides* Sond. in Flora 365 (1857b). Type: South Africa. Western Cape, Cape Town (3318), Hessequas Kloof (-CD), without precise date, ♂ & ♀ plants *Zeyher 3814* (K, lectotype! designated here; BOL!, MO!, NBG!, OXF, PRE!, S!, isolectotypes).

A brittle, decumbent or suberect perennial suffrutex, 20–44 cm, usually growing beneath other shrubs, green to golden-green in overall appearance, rootstock slender. *Stems* woody at base, herbaceous at distal portion, 1–3 mm in diameter, sprawling; glabrous, terete in transverse section, branches decumbent, few at base, but much-branched distally, 5–12 branches, leaves absent or rarely present on branchlets. *Leaves* scale-like, very few to almost absent, adpressed to branchlets, golden to yellowish green, plant surface glabrous, without prominent venation or midrib, apex obtuse, margins fimbriate, straight. *Inflorescence* arranged along the branchlet, spicate, sessile on branchlets; bracts and bracteoles highly reduced to scales; bracts fleshy, 1–1.5 × 0.4–1 mm, triangular, margin entire, obtuse at tips, much shorter than flowers, incurved; bracteoles can easily be confused for bracts, but bracteoles are closely adpressed to flowers, 0.8–1× 0.3–1 mm; flowers campanulate, white, 2–4 × 4–5 mm, 4-merous, external gland absent between perianth lobes; perianth lobe segments 2–3 × 1–3 mm, ovate, obtuse at tips, not distinctly uncinate, seldom lobulate, lobe tube inconspicuous, about 0.2 mm long. Male plant similar to female plants. *Male plant:* branches slender with dense branchlets distally, usually on a slender single stem; internodes 2–6.5 mm long, leaves lax, not imbricate, ovate to triangular, 1–2 × 0.5–1 mm, inflorescences lax; hypanthium tube short to non-existent, shorter than perianth tubes; stamens four, never five; staminal filaments exserted on the walls of perianth lobes at the junctions of the hypanthium tube, about 0.2 mm long. *Female plants:* branches slender, fewer and stouter than male plants; internodes 3.5–7.5 mm long; leaves scant, not imbricate, broadly ovate to triangular, 0.5–1.5 × 0.5–1 mm; inflorescences dense; hypanthium tube inconspicuous, shorter than perianth tubes; style about 0.4 mm long long. *Fruit a* nutlet, ovoid, white, elaiosome absent, 2– 3 × 1–2 mm, without ribs or veins, but surface tends to form wrinkles on drying, persistent perianth segment shorter than fruit (Fig. 3.9).

*Diagnostic characters. – Thesium microcarpum* has been mistaken for *T. fragile* as both plants are brittle, have similar male and female plants, scale-like leaves, and white fruits. *Thesium microcarpum* differs from *T. fragile* in being decumbent or suberect, growing under other smaller shrubs (versus an erect, heath-like plant), branches mainly borne distally,

inflorescences compacted on the branchlets, fruits ovoid, 5-ribbed with faint veins between veins, elaiosome absent (versus branches and inflorescences lax along stem length, fruit truncated, without ribs or veins, but surface wrinkles on drying, elaiosome present), usually found on shale, flat deep sand or sandstones (versus found on sand dunes, sandy soils and coastal sands).

*Distribution and habitat.* – *Thesium microcarpum* has been collected widely across most of the GCFR extending from the Cedarberg Mountains of the Western Cape to Mannetjiesberg in the Eastern Cape (Fig. 3.7C). It occurs on shaley soil, well-drained stony soil, and deep sand to sandstone slopes in Fynbos on gentle mountain slopes of the Cape Peninsula, in Rûens Shale Renosterveld vegetation types or in dry arid regions of the Karoo Mountains, usually under shrubby bushes at elevations between 50 to 700 m above sea level.

*Conservation status.* – *Thesium microcarpum* is a poorly studied taxon (Von Staden, 2015) but is widely distributed across its local habitats and is abundant in nature reserves. Hence, we assessed it as Least Concern (LC), (IUCN Standards and Petitions Subcommittee, 2017).

*Additional materials studied.* – South Africa. EASTERN CAPE: **3326 (Grahamstown):** Base of mountain at Rietvlei, along road to Mannetjiesberg (-BC), 10 Nov 2006, ♂ plants, *Verboom 1149* (BOL). **3324 (Steytlerville):** Plot 74, Baviaanskloof, north of Mountain top, above Enkeldoring (-CB), 20 Sep 2011, ♂ & ♀ plants, *Euston-Brown 1256* (NBG).

WESTERN CAPE: **3218 (Clanwilliam):** Rocherpan Nature Reserve, Relève 23, South end West of track (-CD), 22 Aug 1981, ♂ & ♀ plants, *Rooyen & Ramsey 641* (STE, NBG). **3219 (Wuppertal):** Cederberg mountains, Krakadouwsberg (-AA), 21 Sep 1963, ♀ plants, *Stauffer 5190* (BOL). **3318 (Cape Town)**: Paardeberg, between Wellington and Malmesbury, Vlakfontein, (-DA), 24 Aug 2011, ♂ & ♀ plants, *Nicolson & Roets 287* (NBG); Dassenberg, middle of range, northern slope, Malmesbury (-DA), 11 Sep 1979, ♀ plants, *Boucher 4701* (NBG, STE); Helderfontein farm, Malmesbury (-DA), 11 Sep 1979, ♀ plants, *Boucher 4441* (NBG, STE). **3319 (Swellendam):** Rivierzondereinde, at Stormvallei, Hassaquaskloof and Breederivier (-CD), 01 Nov.1989, ♂ & ♀ plants, *Zeyher 3814* (HBG). **3320 (Montagu)**: Dobbelarskloof, hillside, Montagu (-CC), 25 Sep 1946, ♀ plants, *Lewis 3397* (MO); near Barrydale, Swellendam (-CD), 05 Aug 1949, ♂ plants, *Morris 171* (NBG/BOL); Little Namaqualand Bend from Komaggas mountains (-DB), 02 Jul 1926, ♂ plants, *Marloth 6950* (STE); East of Anysberg West of Ladismith (-DA), 05 Oct 1982, ♀ plants, *Van Wyk* 994 (NBG,

STE); Headlands along coastline, S of Pacaltsdorp, southern slopes of Rooiklip headlands (-DD), 14 Aug 1993, *Victor 231* (PRE); Montagu (-CD), 06 Oct 1993, ♂ & ♀ plants, *Esterhuysen 37357* (NBG). **3321 (Ladismith):** 2 miles on Port Elizabeth side of Schoenmakerskop, (-AB), 30 Sep 1963, ♀ plants, *Wells 2699* (PRE); Klein Swartberg, ca. 1 km north of Seweweekspoort, near Ladismith (-AD), 26 Nov 2007, ♀ plants, *García, Gonzalez et al. 3946* (NBG); Touwsberg, W end summit ridge, on dry rocky slopes (-DB), 05 Oct 1993, ♂ & ♀ plants, *Oliver 10319* (STE, NBG); Klein Swartberg, just after turnoff for Rocklands, Towerkop Nature Reserve (-AD), 26 Nov 2007, ♀ plants, *García, Gonzalez et al. 3947* (NBG). **3322 (Oudtshoorn):** Ouhangsberg (-CC), 07 Nov 1992, *Oliver 10260* (STE); Boomplaas Cango valley, (-CB), 21 Jan 1976, ♀ plants, *Hugo 8* (BOL); Buffel rivier, below Kammanassieberg (-DB), 03 Oct 1971, ♂ plants, Thompson 1374 (NBG, STE). **3323 (Willowmore):** Tsitzikamma mountains, Uniondale (-AD), 01 Mar 1950, ♂ & ♀ plants, *Esterhuysen 16848* (BOL), Kammanassie, Uniondale (-AC), 31 Jan 1941, ♀ plants, *Esterhuysen 4702* (NBG/BOL); Buffelsberg, Kammanassie Mountains (-DB), 29 Oct 1983, ♂ plants, *Viviers & Vlok 17* (STE). **3418 (Simonstown):** Rooikrans, Fynbos Private Nature Reserve (-AA), no precise date, *Stirton 13844* (BOL). **3420 (Bredasdorp):** Plaatjieskraal Farm, Overberg (-AA), 22 March 2017, ♂ and ♀ plant, *Zhigila & Muasya 149* (BOL); Kykoedie Farm, 30 km from Bredasdorp to Stormsvlei (-AD), 01 Nov 2011, *Stirton & Muasya 13434* (BOL); Plaatjieskraal Farm, upper parts of Sonderkoskop, along jeep track and slopes in the reserve (-AD), 11 Sep 2017, ♂ and ♀ plant, *Zhigila & Muasya 150* (BOL); Nysti Farm, 40 km from Bredasdorp to Swellendam (-AD), 2 Nov 2011, ♀ plant, *Stirton & Muasya 13445* (BOL); De Hoop Nature Reserve, Windhoek (-AD), 17 Mar 1977, ♂ & ♀ plants, *Thompson 3471* (NBG, STE). **3421 (Riversdale):** hills near the Gouritz River (-CD), no precise date, ♂ & ♀ plants, *Schlechter 9433* (K); Hills south of Vermaklikheid (-AC), 24 Nov 1972, ♂ & ♀ plants, *Oliver, 4168* (NBG, STE); On main road 2 km East of Resiesbaan siding (-AB), 28 Aug 1979, ♂ & ♀ plants, *Bohnen 6242* (NBG, STE). **3422 (Mossel Bay):** Groot Brak River, George Division (-CB), 08 Aug 1931, ♂ & ♀ plants, *Thorne s.n.* (MO 51725); On trail near beach, above parking area, Knysna District, Goukama (-BB), 10 Jun 2008, *Moore 52* (NBG); Groot-Swartberg, along R314 ca 3.6 air km S of Klaarstroom, hills above rest area, at Peraboom Drif (-CD), 27 Nov 2007, ♂ & ♀ plants, *García 3953* (NBG); Boomplaas, Cango Valley (-AC), 29 Feb 1974, ♂ & ♀ plants, *Moffett 302* (NBG, STE). **3423 (Knysna):** along R340, ca. 8 km N of junction with N2, near Wittedrif (-AA), 04 Jun 2017, ♂ & ♀ plants, *Zhigila 106* (BOL); Noetsi River, W side (-AA), 22 May 1984, ♂ & ♀ plants, *Callaghan & Van Wyk 53* & *78* (NBG, STE).

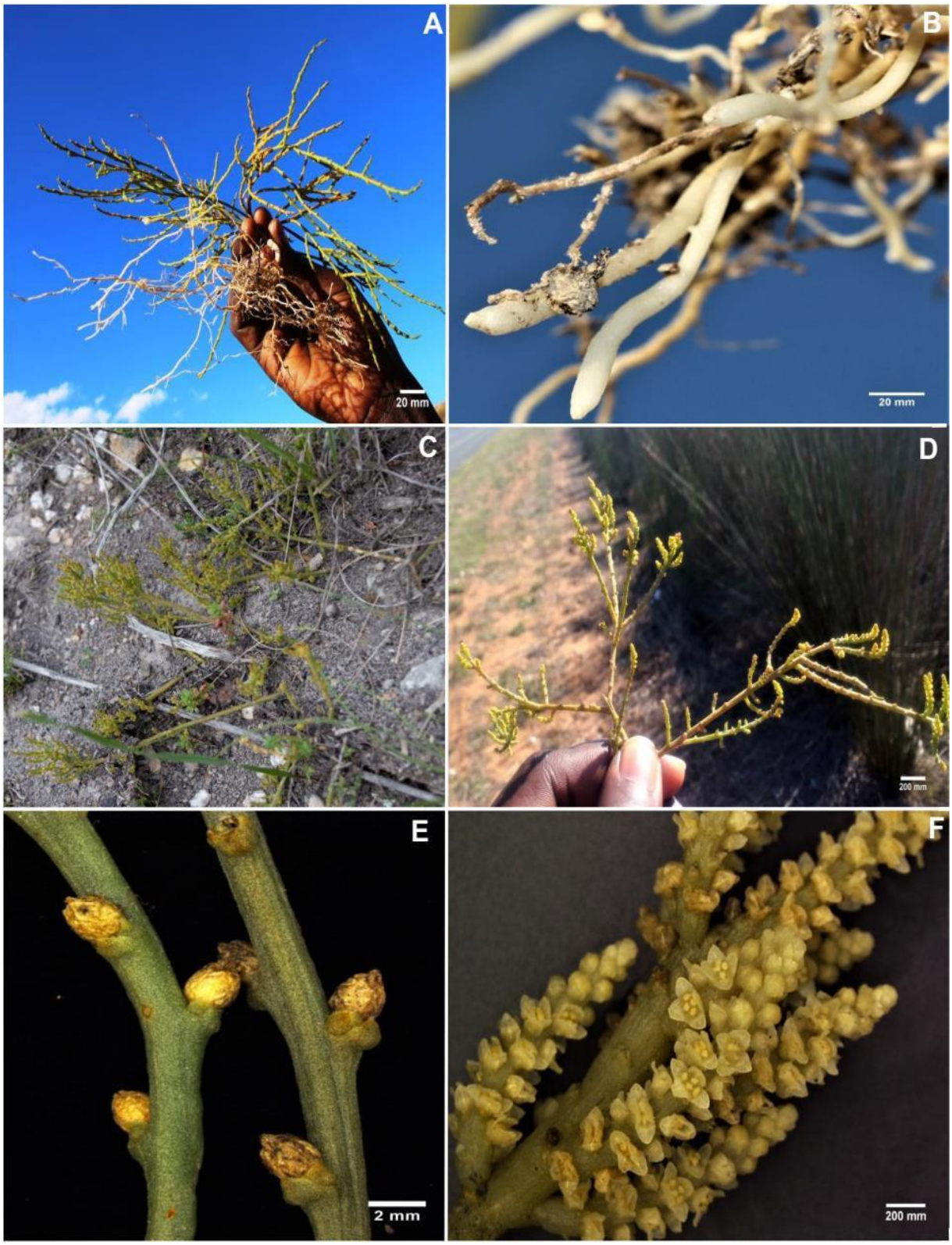



**Fig. 3.12:** *Thesium microcarpum*: (A) a view of male plant displaying its slender rootstock, (B) closer view of slender rootstock, (C) habit and substrate of sprawling male plants, (D) detailed view of male plant, (E) female fruiting shoot, (F) branchlets with dense flowers in male plants. Photographs: Daniel Zhigila

**3.6.1.6.** ***Thesium minus*** (A.W.Hill) J.C.Manning & F.Forest, in Bothalia 43(2): 215 (2013). ≡ *Thesidium minus* A.W.Hill in Bull. Misc. Inform. Kew 3: 98 (1915). Type: South Africa. Western Cape, Caledon Division, Houw Hoek (-3419), 380 m, without precise date, ♂ and ♀ plants, *Schlechter 9431*, 380 m (K! Lectotype, designated here; S!, BOL!, PRE!, NBG!, STE! and SAM! Isolectotypes). *Schlechter 9431* is designated as lectotype, since both male and female plants are mounted on the same herbarium sheet, the locality is within the typical geographical range of the taxon, and it was cited by Hill (1925) and best fits the protologue.

An erect heath-like annual plant, 5–10 cm tall, yellowish green in general appearance, plant not brittle, stout fibrous rootstock, branches attached mainly to the rhizome, 4–12 branches; branching pattern virgate, leaves may or may not subtend branchlets. *Stems* herbaceous in aerial portion, 0.5–1.2 mm in diameter, erect, glabrous, prominently sulcate in transverse section. *Leaves* well-developed, upcurved to adpressed to the branchlets, green, glabrous, without a prominent midrib, veins parallel, apex acute, margins entire, concave or convex to straight. *Inflorescences* in branchlet axils along the main branches, composed of a dichasial (2 or 3 flowered) cyme, shortly pedicellate; bracts and bracteoles leaf-like; bracts fleshy, 2.5–5 × 0.5–1 mm, linear-lanceolate, margins entire, green, acute at tips, longer than the flower, straight; bracteoles bract-like, but smaller, 1.5–3 × 0.5–1 mm; flowers campanulate, green, 1–2.5 × 0.5–1.5 mm, 4-merous, perianth lobe external glands absent, perianth lobe segments 0.6–1.4 × 0.5–0.8 mm, lobes ovate to triangular, obtuse or subacute at tips, not distinctly uncinate, somewhat lobulate; tube about 0.4 mm long; male and female plants well differentiated. *Male plants*: branches more slender than female plants, internodes wider than female plants, 2.5–8 mm; leaves sparse, not imbricate, narrower than in female plants, linear to acicular, 5–10 mm × 0.5–1 mm; inflorescences lax; hypanthium tube short to non-existent; stamens four, staminal filaments exserted at the junction of hypanthium and perianth tube, about 0.2 mm long. *Female plants*: branches more robust, internodes shorter, 1.5–2.5 mm; leaves denser than in male plants, imbricate, linear, 7.5–13 × 0.4–1 mm; inflorescences a 3-flowered cyme; hypanthium length shorter than perianth lobes; style short, about 0.2 mm long. *Fruit* a nutlet, ovoid, green, attached to the branch by a swollen pedicel to form a white attenuated elaiosome, 1.5–2.5 × 1–2 mm, conspicuously 10-ribbed with prominent reticulate veins between the longitudinal ribs, capped with green persistent perianth lobe segments, shorter than the fruit (Fig. 3.14).

*Diagnostic characters.* – *Thesium minus* is very similar to *T. fruticulosum* in its glabrous plant surface, multi-stemmed basal parts, terete stems, fastigiate branching pattern, leaves without a conspicuous midrib, bracts and bracteoles that are leaf-like and flowers that are

attached to the branchlet by a short to non-existent pedicel. *T. minus* differs from *T. fruticulosum* in being annual, with a fibrous rootstock, 5–10 cm in height, (versus perennial suffrutex, simple tap root system, to about 30 cm long), leaves in male plants more slender (versus leaves similar in both male and female plants), internodes wider, 2.5–8 mm wide (versus internodes shorter in both male and female plants, 0.2–2 mm long), fruit elaiosomes absent, rarely present (versus fruit elaiosomes present).

*Distribution and habitat.* – *Thesium minus* occurs in Fynbos on mountains of the Caledon, Bredasdorp and Riversdale divisions of the Western Cape Province and as far east as Grahamstown in the Eastern Cape Province (Fig. 3.7D). It is usually found in open vegetation on sandstones or quartzite soils from 300 to c. 700 m above sea level.

*Conservation status.* – Von Staden (2015) assessed *T. minus* as a data deficient taxon and considered it taxonomically problematic. She viewed the species as under-studied and that it can easily be confused with *T. fruticulosum*. In our assessment, *T. minus* is rare in its major habitats and may be found in protected reserves only. We therefore evaluated the species as Rare following the IUCN Standards and Petitions Subcommittee (2017) guidelines.

*Additional specimens studied.* – South Africa. EASTERN CAPE: **3325 (Port Elizabeth)**: Port Elizabeth (-CB), 11 Oct 1931, ♂ & ♀ plants, *Holland 3690* (BOL); Regio occidentalis, in montibus prope Vogelgat (-BA), 15 Jan 1961, ♂ & ♀ plants, *Esterhuysen 5214* (HBG, BOL). **3326 (Albany)**: Grahamstown Nature Reserve (-AD), 20 Sep 1963, ♀ plants, *Staufer 5180* (BOL); Grahamstown Nature Reserve (-AD), 02 Dec 1977, *Hillard 10829* (NBG).

WESTERN CAPE: **3319 (Worcester):** North stop, between Michell Park and Delville, Worcester (-AD), 16 Jan 1961, ♂ & ♀ plants, *Esterhuysen 28741* (BOL). **3323 (Willowmore):** West of Joubertina (-DD), 17 Nov 1958, ♀ plants, *Acocks 20025* (PRE). **3418 (Simonstown):** Harold Porter Botanic Garden (-BD), 14 Jan 1976, ♂ plant, *Brenan 14051*, ♀ plant, *Brenan 14050* (NBG); Lake Pleasant hotel, Knysna Division (-DD), 06 Aug 1960, *Acocks 21308* (PRE). Mountains East of Steenbras River (-BC), 02 Jan 1921, *Marloth 10074* (PRE). **3419 (Caledon)**: Houw Hoek (-AA), 26 Nov 1898, ♂ & ♀ plants, *Schlechter 9432* (PRE); Houw Hoek, in montibus (in mountains), 26 Nov 1897, *Schlechter 9431* (PH, BOL); Vogelgat, above Dragonfly Pool (-AD), 08 Apr 1987, ♂ & ♀ plants, *Williams 3795* (NBG), Collibus (hills), Riet Fontein, Elim (-AB), 09 Dec 1896, *Bolus 8601* (K, BOL); Houw Hoek, railway line (-AB), 29 Sep 1970, *Esterhuysen 32490a* (BOL); Vogelgat, above Dragonfly Pool (-AD), 8 Apr 1987, ♂ plant, *Williams 3794* (NBG).


**Fig. 3.13:** *Thesium minus*: (A) post-fire habit, based on *Esterhuysen 32490a* (K!), (B) detailed rhizome and roots, (C) male flowering shoot, (D) a female fruiting shoot, (E) fruits. Photographs: Daniel Zhigila.

**3.6.1.7. *Thesium quartzicolum*** Zhigila, Verboom & Muasya **sp. nov.**

Type: South Africa, Overberg, Western Cape, Bredasdorp Division (3420), Spitskop farm (-BC), (34°18'5.91"S and 20°17'5.90"E), on quartz patches in Renosterveld vegetation, 22 March 2017, ♂ & ♀ plants *Zhigila & Muasya 026,* (BOL, holotype!; K!, NBG!, PRE!, isotypes).

An erect annual herb, 8–15 cm tall, heath-like, yellowish to golden-green in appearance, plant brittle, with a fibrous rhizome, scarcely branched, 3–10 jointed branches, branching pattern virgate, leaves subtending branchlets. *Stems* woody at base, herbaceous above, 1–3 mm in diameter, erect, glabrous, terete in transverse section. *Leaves* sparingly distributed and reduced to scales, decurrently adpressed to the stem, golden-green, plant surface glabrous, no prominent venation or midrib, leaf apex subacute to obtuse, margin cartilaginous and ciliolate, straight, glabrous, fleshy, apex obtuse to subacute. *Inflorescences* distributed along the branch length, spikes in branchlet axils, sessile or attached to the stem by a short to non-existence pedicel; bracts and bracteoles scale-like; bracts fleshy, 0.8–2.5 × 1–2 mm, broadly subrotund, margins cartilaginous, acute at tips, much shorter than the flower, usually adpressed; bracteoles bract-like, but smaller, 0.7–2.5 × 0.5–1.5 mm; flower shape campanulate, green to golden green, 3–5 × 2–4 mm, 4-merous, external gland between perianth lobes absent, perianth lobe segments 2–3.5 × 1–2.5 mm, ovate to lanceolate, obtuse at tips, rarely acute, not distinctly uncinate, not lobulate; tube short, 0.2–0.3 mm long. Male plants similar to female plants. *Male plants:* branches slender and sparingly arranged along the stem length, internodes 3–6 mm; leaves lax, not imbricate, broadly ovate to triangular, 1–2 × 0.5–0.8 mm; inflorescences lax; hypanthium tube conspicuous, shorter than perianth tube; stamens four, never five, staminal filaments distinct to connately exserted at junction of hypanthium and perianth tube, about 0.2 mm long. *Female plants* are stouter and branches woodier than male plants, internodes 4–8 mm; leaves lax, not imbricate, broadly ovate to triangular, 0.5–1.5 × 0.5–0.8 mm; inflorescences lax; hypanthium tube shorter than the perianth tubes; style about 0.3 mm long. *Fruits* nutlets, ovoid to globose, green to golden-green, elaiosome absent, 1.2–3 × 1–2.5 mm, without ribs, veins inconspicuous, capped with green persistent perianth lobe remnants, shorter than fruit (Fig. 3.10).

*Diagnostic traits. – Thesium quartzicolum* is similar to *T. fragile* with which it shares traits such as growth form, plants brittle, heath-like, branching pattern virgate, male and female plants very similar, leaves scanty, scale-like, subtending each branchlet, and few-flowered spikes. It has several striking morphological traits distinguishing it from *T. fragile*, including being an erect annual herb up to about 8–15 cm tall (versus erect perennial suffrutex, 10–40 cm tall), rhizome slender (versus woody), stems terete, about 2 mm thick (versus sulcate or

subangled, 2–4 mm thick), fruits globose to ovoid, golden-green, sessile without elaiosome (versus truncated), perianth segments green, persistent (versus perianth remnants white, yellow or orange), usually found on silcrete-quarzitic soils (versus normally found in sandy coastal areas).

*Distribution and habitat.* – *Thesium quartzicolum* is a narrow endemic restricted to the silcrete-quartz outcrops of the typical Renosterveld scrub of the Overberg (Fig. 3.7E, solid triangles) and known from three localities at elevation between 200 and 300 m above sea level.

*Etymology.* – The specific epithet means 'quartz dwelling' and alludes to its preference for the quartzite soils of the Overberg Renosterveld.

*Conservation status.* – Although concerted efforts were made to find more populations, no other populations could be found. Therefore, further botanical surveys should be conducted to explore whether more populations exist. Potentially, its geographical range is restricted to the Renosterveld quartz patches of the Overberg. These patches are considered Critically Endangered habitats (Raimondo et al., 2009), as 95% of the landmass is currently under cultivation (Curtis et al., 2013; Curtis, 2017). Also, large mammals graze on *T. quartzicolum* (Zhigila pers. obs.), which may negatively impact its population given that remnant Renosterveld patches are used for livestock rearing. As *T. quartzicolum* is endemic to Overberg Renosterveld patches, we assess it as Critically Endangered (CR, B2) under the South African Red list categories and criteria (Raimondo et al., 2009) and IUCN Standards and Petitions Subcommittee (2017) guidelines.

*Additional specimens examined.* – South Africa. WESTERN CAPE: **3420 (Bredasdorp):** W. flank of S**.** Spitskop private farm slopes (-BC), 22 March 2017, ♂ & ♀ plants, *Zhigila & Muasya 023* (BOL, K, NBG); S. Spitskop, on quartz patches, Renosterveld vegetation (-BC), 23 March 2017, ♂ & ♀ plants, *Zhigila & Muasya 024, 026* (BOL, K, NBG); S.W flank slopes of Milanskraal Farm (-BA), 25 March 2019, ♂ & ♀ plants, *Zhigila 278* (BOL, NBG); E. flank of N**.** Spitskop hills, across private farm (-BB), 26 March 2019, ♂ & ♀ plants, *Zhigila 287* (BOL, NBG).

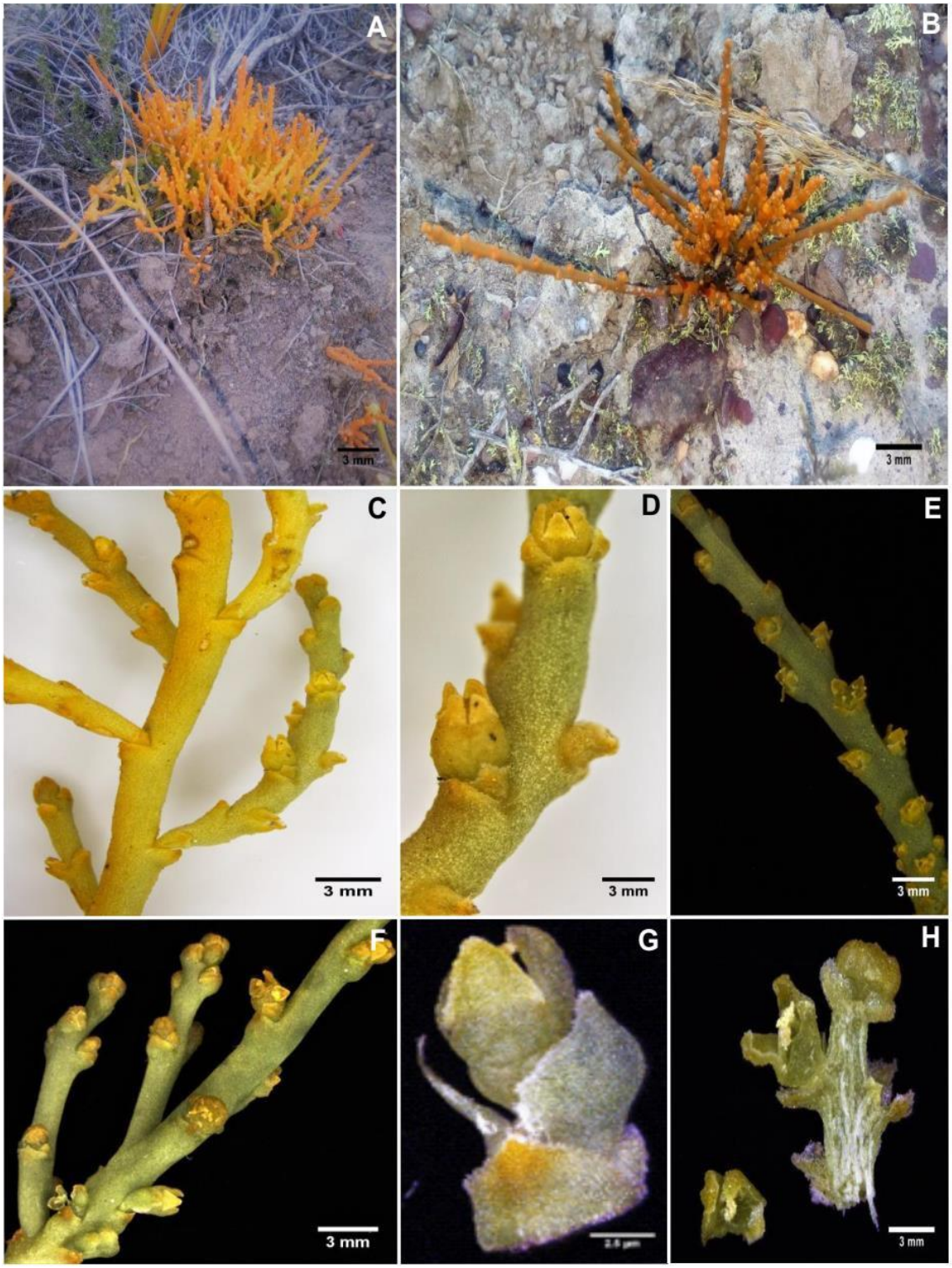



**Fig. 3.14:** *Thesium quartzicolum*: (A) habit and substrate of female plants, (B) habit and quartz-silcrete substrate of male plants, (C) an amplified view of female plants displaying fruiting jointed branchlets, (D) a shoot showing scale-like bracts and bracteoles subtending fruits, (E) a male shoot displaying 4-merous flowers with clear stamens, (F) female flowering twig, (G) detailed floral parts in relation to scaly leaf, cartilaginous bract and bracteole margins, (H) longitudinal section of floral parts. Photographs: Daniel Zhigila.

### 3.6.2. Notes on uncertain taxa

**3.6.2.1.** ***Thesium confusum*** J.C.Manning & F.Forest mentioned in Bothalia 43:2 (2013) *Thesidium fragile* Sond. in Flora: 364 (1857a), non *Thesium fragile* L.f. (1782).

We were not able to locate any specimens stored under the name '*T. confusum*', and thus excluded *T. confusum* from this treatment. Von Staden (2015), who was also uncertain as to its provenance, assessed its conservation status as data deficient and viewed it as conspecific with *T. fragile*.

**3.6.2.2.** ***Thesium leptostachyum*** A.DC. in DC. Prodr. 14:674 (1857b) *Thesidium leptostachyum* Esp. Nouv. Thesium: 5 (1857a). *Thesidium leptostachyum* (A.DC.) Sond. in Flora, 405 (1857b). Type: South Africa. Western Cape, Knysna Division; Karratera River (3326AD), ♂ plant, Drège 8173 (K!, holotype! NBG!, SO! isotypes).

The position of *T. leptostachyum* was not based on data from this study as all efforts to collect or locate materials of this taxon were unsuccessful. We based the taxonomic treatment on the type specimen, description from the author (De Candolle, 1857b) and other previous studies (Hill, 1925; Forest and Manning, 2013) in terms of nomenclature, geographical range (Fig. 3.7F, circles) and key placement in section *Heteromorpha*. For species descriptions and paratypes, see Hill (1925).

# CHAPTER FOUR

## 4.0 Six new *Thesium* (Santalaceae) species endemic to the Greater Cape Floristic Region, South Africa, and one new name

### 4.1 INTRODUCTION

South African *Thesium* species were last revised almost a century ago (Hill, 1925), since which the number of collections has grown, and several new species have been described (*e.g.* Compton 1931; Brown, 1932; Levyns, 1950; Brenan, 1979; García et al., 2018), rendering Hill (1925)'s taxonomy outdated. There is therefore a clear need for a major revision of the South African *Thesium* species (SANBI, 2017). Although two groups — the grassland *T. goetzeanum*-complex with nine species (Visser et al., 2018) and *Thesium* sect. *Hagnothesium* DC (1857a: 4) with eight species (Zhigila et al., 2019a) — have recently been revised, the species-rich (ca. 103 species) Cape clade (sensu Moore et al., 2010) remains in need of revision (see Moore et al., 2010, Visser et al., 2018, Zhigila et al., 2020 for details of taxonomic history). Sadly, a comprehensive revision of the entire genus, or even of just the Cape clade, is unlikely to be completed soon. This is due to the large number of species, and the extreme morphological complexity of this genus.

Many Cape *Thesium* species have very small ranges (Hill, 1925, Moore et al., 2010) and some of these local endemics associate strongly with threatened habitats (Manning and Goldblatt, 2012, http://redlist.sanbi.org/). One example is the Shale Renosterveld within the Fynbos Biome in the GCFR (Mucina and Rutherford, 2006; http://redlist.sanbi.org/). The Eastern Rûens Shale Renosterveld of the Overberg is one of the richest Mediterranean-type ecosystems globally, and it is critically endangered (Raimondo et al., 2009; Von Staden 2015; Topp and Loos, 2019), with 95% of its landscape currently under cultivation (Curtis et al., 2013; http://redlist.sanbi.org/). The remainder comprises of pockets of agriculturally-unsuitable habitats that are scattered on private farms (Curtis et al., 2013). Unfortunately, these pockets of Renosterveld, which are typically used for grazing, have been poorly botanised owing to their inaccessibility. During field trips conducted to several such pockets of Renosterveld and Fynbos vegetation between March 2007 and October 2018, we discovered undoubtedly novel *Thesium* species that differed from all known species in several traits. Taking into account that a full revision of the Cape *Thesium* clade is unlikely to be completed in the near future, and the threatened nature of these species, it is critical that they be formally described for conservation and infrageneric classification purposes. The objectives of this chapter are therefore to (i) describe six new species as *Thesium aspermontanum* Zhigila, Verboom & Muasya , *T.dmmagiae* Zhigila, Verboom & Muasya, *T. neoprostratum* Zhigila, Verboom & Muasya, *T.*

*nigroperianthum* Zhigila, Verboom & Muasya, *T. rhizomatum* Zhigila, Verboom & Muasya, and *T. stirtonii* Zhigila, Verboom & Muasya; (ii) elevate *Thesium assimile* Sonder (1857: 360) var. *pallidum* Sonder (1857: 360) to species rank and provide it with a new name as *T. sawae* Zhigila, Verboom & Muasya; (iii) provide a taxonomic circumscription for each species; (iv) determine and describe the geographical ranges of the seven species based on existing and new distribution data; and (v) provide a preliminary assessment of the conservation status of each species.

## 4.2 MATERIALS AND METHODS

A comparative study was carried out using specimens housed at BOL, FHO, K, MO, NBG (including SAM and STE), OXF and PRE (Thiers, 2019), and online digital images of type specimens (JSTOR, 2019). Additional specimens were identified in the field using existing taxonomic keys (Hill, 1915; 1925). For descriptive purposes, the floral terminologies of Hill (1925) and Visser et al. (2018) were used, while the designation of taxon names was done in accordance with the latest *International Code of Nomenclature for algae, fungi and plants* (Shenzhen Code, Turland et al., 2018). Where necessary, morphological characters were observed and scored using a hand lens (10x) or stereomicroscope (Nikon Stereoscopic Zoom Microscope SMZ1500 fitted with Nikon DS-5M Camera). Measurements were done using a hand ruler, digital calliper or a dissecting microscope fitted with an eye-piece graticule. Holotypes of the newly described species were deposited in BOL, with isotypes having been distributed to K, NBG, and PRE. All specimens cited in this paper have been examined.

Species distribution maps were generated in R version 3.6.1 (R Core Team, 2019) using the raster package version 2.6-7 (Hijmans, 2017). Specimen localities were allocated to at least quarter degree grid cells following the gazetteer provided by Leister and Morris (1976) and/or topographical maps at a scale of 1: 50 000. The preliminary red list status for each species was determined using the methodology provided in the *Plant Red List of South Africa* (Raimondo et al., 2009), as well as the conservation assessment criteria provided in the IUCN guidelines (IUCN, 2017). The extent of occurrence (EOO) and areas of occupancy (AOO) of individual species were assessed using the software GeoCAT (2018), with the resolution dependent on a recommended 2 × 2 km matrix (Bachman et al., 2011; IUCN, 2017).

## 4.3 RESULTS

In the context of a lineage-based species concept, six putative new species (*T. aspermontanum, T. dmmagiae, T. neoprostratum, T. nigroperianthum, T. rhizomatum* and *T. stritonii*) are described, each of which is morphologically and geographically cohesive. In addition, the data raised *T. carinatum* var. *pallidum* to the species level, as *T. sawae*. The data highlighted some discontinuous characters delimiting these from known *Thesium* species (Tables 4.1 and 4.2). The life form of species described here are perennial and shrubby (*e.g. T. aspermontanum*) or the subterranean parts are perennial with annual and herbaceous aerial shoots (*e.g.* in *T. rhizomatum*). Although growth form varies among species, it can be broadly categorized as erect (*e.g. T. aspermontanum*), to suberect (*e.g. T. sawae*) or decumbent (*e.g. T. neoprostratum*) (Tables 4.1 and 4.2). The branching patterns are variable among the species, ranging from sympodial in *T. aspermontanum,* to virgate in *T. stirtonii* to intricate as in *T. sawae* (Fig. 4. 1). The leaves are either well-developed (elongate) as in *T. sawae* or reduced to scale-like structures as in *T. nigroperianthum*, alternate, adpressed to the stem or spreading, and terete, triangular or with clearly differentiable adaxial and abaxial surfaces (Table 4.2). The flowers are patelliform, hypocrateriform or urceolate, often with trichomes on the perianth lobe apices like in *T. dmmagiae* or glabrouslike in *T. aspermontanum* (Table 4.1).

Most of the species described here are strong edaphic specialists, being associated with just a single geology and vegetation type. Four (*T. dmmagiae, T. nigroperianthum, T. rhizomatum,* and *T. stirtonii*) are confined to unique edaphic microhabitats associated with outcrops in the Eastern Rûens Shale Renosterveld (Fig. 4.2). *Thesium aspermontanum*, however, is restricted to granite-derived soils of the Skurweberg Mountains (Fig. 4.2), while *T. sawae* and *T. neoscabrum* occupy quartzitic and shaley substrates in mountain Fynbos vegetation. With respect to conservation status, species described in this study fall into various threat categories, except for *T. nigroperianthum*, which is preliminarily considered to be of "Least Concern". We view *T. neoprostratum* as "Endangered", *T. sawae* as "Vulnerable" and *T. dmmagiae* as "Data Deficient" pending the collection of further survey data. Three species, *T. aspermontanum T. rhizomatum* and *T. stirtonii* are classified as "Critically Endangered".

**Table 4.1a**: Comparison of the major diagnostic traits isolating the newly-described species (A. *Thesium aspermontanum*, B. *T. dmmagiae*, C. *T. neoprostratum* and D. *T. sawae*) and their most-similar congeners. Characters not seen are indicated with an "?".

| **A** | ***T. aspermontanum*** | ***T. nautimontanum*** | ***T. subnudum*** |
|---|---|---|---|
| Branching pattern | sympodial | sympodial | virgate |
| Plant height | up to 50 cm | up to 40 cm | up to 70 cm |
| Plant colour | green and spotted with red or maroon | green, unspotted | straw-coloured, unspotted |
| Leaves | lanceolate, ca. 5 mm long | scale-like, ca. 1.5 mm long | acicular, ca. 5.0 mm long |
| Inflorescences | corymb, 4–5-flowered cymules | elongated terminal spike | elongated terminal spike |
| Old floret colour | red to maroon | ? | ? |
| Perianth lobe apical trichomes | absent | absent | present |
| Distribution | Skurweberg Mountain | Matroosberg Mountain | wide spread in the GCFR |
| **B** | ***T. dmmagiae*** | ***T. pubescens*** | ***T. frisea*** |
| Habit | decumbent | erect to suberect | erect to suberect |
| Stem and leaf surfaces | scabrid | pubescent | glabrous |
| Leaf length (mm) | 4.0–10 | 10–25 | 10–15 |
| Leaf shape | triangular or terete | terete | terete |
| Leaf aspect | straight | recurved | straight |
| Inflorescence type | paniculate | globose spike | elongated spike |
| Perianth lobe apex | not uncinate | not uncinate | distinctly uncinate |
| **C** | ***T. neoprostratum*** | ***T. prostratum*** | |
| Growth habit | decumbent | decumbent | |
| Leaf shape | acicular | acicular to linear | |
| Leaf length (mm) | 2.0–3.0 | 2.0–5.0 | |
| Leaf margin | ciliate | entire | |
| Perianth lobe apical trichomes | present | absent | |
| Fruit surfaces | 5-ribbed, faintly reticulate | 10-ribbed, conspicuously reticulate | |
| **D** | ***T. sawae*** | ***T. carinatum*** | ***T. viridifolium*** |
| Growth habit | decumbent or suberect | erect | erect |
| Plant height | up to 25 cm | up to 50 cm | up to 50 cm |
| Branching pattern | intricate | virgate | virgate |
| Plant colour | multi-coloured | green | green |
| Old florets | white | coffee brown | coffee brown |
| Leaf margins | scarcely scabrid | entire | entire |

**Table 4.1b:** Major diagnostic traits isolating the new species (A. *Thesium nigroperianthum*, B. *T. rhizomatum* and C. *T. stirtonii*) from their most-similar congeners

| **A** | ***T. nigroperianthum*** | ***T. stirtonii*** | ***T. leptocaule*** | ***T. nigromontanum*** |
|---|---|---|---|---|
| Habit | decumbent or suberect | decumbent or suberect | erect | erect to suberect |
| Rootstock | woody | non-woody | non-woody | non-woody |
| Stem surface | spotted | spotted | not spotted | not spotted |
| Branchlet type | flowering and non-flowering | flowering and non-flowering | flowering | flowering |
| Leaves | scale-like | scale-like | two types, acicular at base, scale-like at the apex | two types, linear at base, lanceolate at the apex |
| Inflorescence types | paniculate, often corymbose | paniculate, often corymbose | lax cyme, 3-dichasial | axillary cymules, to sub-corymbose |
| Perianth external glands | conspicuous | conspicuous | inconspicuous | conspicuous |
| Perianth lobe apices | black | cream to green | black | black |
| **B** | ***T. rhizomatum*** | ***T. minus*** | | |
| Sexual system | hermaphroditic | dioecious | | |
| Inflorescence type | corymb, 5–7-flowered heads | spike, monochasial in branch axils | | |
| Perianth lobe apex colour | creamy green | green | | |
| Perianth external glands | inconspicuous | absent | | |
| Habitat | shaly Renosterveld or ecotone of Renosterveld and limestone | sandstone mountain Fynbos or coastal slopes | | |
| **C** | ***T. stirtonii*** | ***T. flexuosum*** | ***T. leptocaule*** | ***T. nudicaule*** |
| Habit | decumbent or suberect | decumbent or suberect | erect | erect |
| Rootstock | woody | slender | slender | slender |
| Branchlet type | flowering and non-flowering | flowering | flowering | flowering |
| Leaves | scale-like | scale-like | leaf-like, dimorphic: acicular at base, lanceolate at apex | scale-like |
| Inflorescence type | panicle | spike | lax cymose spike | spike |
| Perianth external glands | conspicuous | inconspicuous | inconspicuous | conspicuous |
| Perianth lobe apical trichomes | absent | present | absent | absent |
| Bract apex colour | brown | green | black | black |

## 4.4 DISCUSSION

Six undescribed species (*T. aspermontanum, T. dmmagiae, T. neoprostratum, T. nigroperianthum, T. rhizomatum* and *T. stritonii*) are presented, each of which is morphologically and geographically cohesive. The lineage-based species concept of de Queiroz (2007) was adopted to delimit these taxa. This concept admits the use of several lines of evidence, including reproductive, genetic, morphological, geographical, and ecological to distinguish species. In the absence of reproductive and genetic data, we relied largely on morphological and geographical evidence to delimit these species. In the context of this species concept, the study sought to identify two or more morphological traits that differ consistently between putative new species and so provide evidence of their reproductive isolation (Grismer, 2001; de Queiroz, 2007). Historically important diagnostic morphological characters in *Thesium* include the branching patterns (Fig. 4.1; Hill, 1915; 1925), which can be decumbent as in *T. dmmagiae* or intricate as in *T. sawae*. The stems may be terete, grooved or winged in transverse sections (Hill, 1915; Visser et al., 2018). The leaves are either well-developed (elongate) as in *T. sawae* or reduced to scale-like structures as in in *T. nigroperianthum*, adpressed to the stem or spreading, and terete, triangular or with clearly differentiable adaxial and abaxial surfaces (Hill, 1915; Table 4.2). Flowers are generally 5-merous, with some forms of teratological polymorphisms (Hill, 1915; Forest and Manning, 2013), and patelliform, hypocrateriform or urceolate, often with trichomes on the perianth lobe apices as in *T. dmmagiae* or glabrous a in *T. aspermontanum* (Table 4.1). The fruits are nutlets or drupes and are typically capped by remnants of perianth lobe segments (Hill, 1915).

The microhabitats associated with outcrops in the Eastern Rûens Shale Renosterveld harbours four of the six species described here. These habitat remnants account for the remaining 5% of the Overberg landscape (Topp and Loos, 2019). Like the quartz outcrops of the Succulent Karoo (Schmiedel and Jürgens, 1999), these outcrops are considered hotspots of plants endemism (Curtis et al., 2013; SANBI, 2017). *Thesium aspermontanum*, however, is restricted to granite-derived soils of the Skurweberg Mountains (Fig. 4.2), while *T. sawae* and *T. neoscabrum* occupy quartzitic and shaley substrates in mountain Fynbos vegetation. That these species are threatened is unsurprising given that they are endemic to the Overberg Renosterveld, a habitat considered as Critically Endangered (Von Staden, 2015). Although the Overberg Renosterveld is severely fragmented due to farming activities, it comprises the largest and most intact component of the Renosterveld biome (Curtis et al., 2013; Topp and Loos, 2019). This critically endangered Renosterveld ecosystem (Von Staden, 2015, Topp and Loos, 2019) harbours the greatest number of endemic plant species in the GCFR (Curtis et al., 2013;

SANBI, 2017). It is one of the last remaining species diversity hotspots in the Overberg due to its heterogenous geomorphological attributes, diverse climatic and edaphic variables (Topp and Loos, 2019).

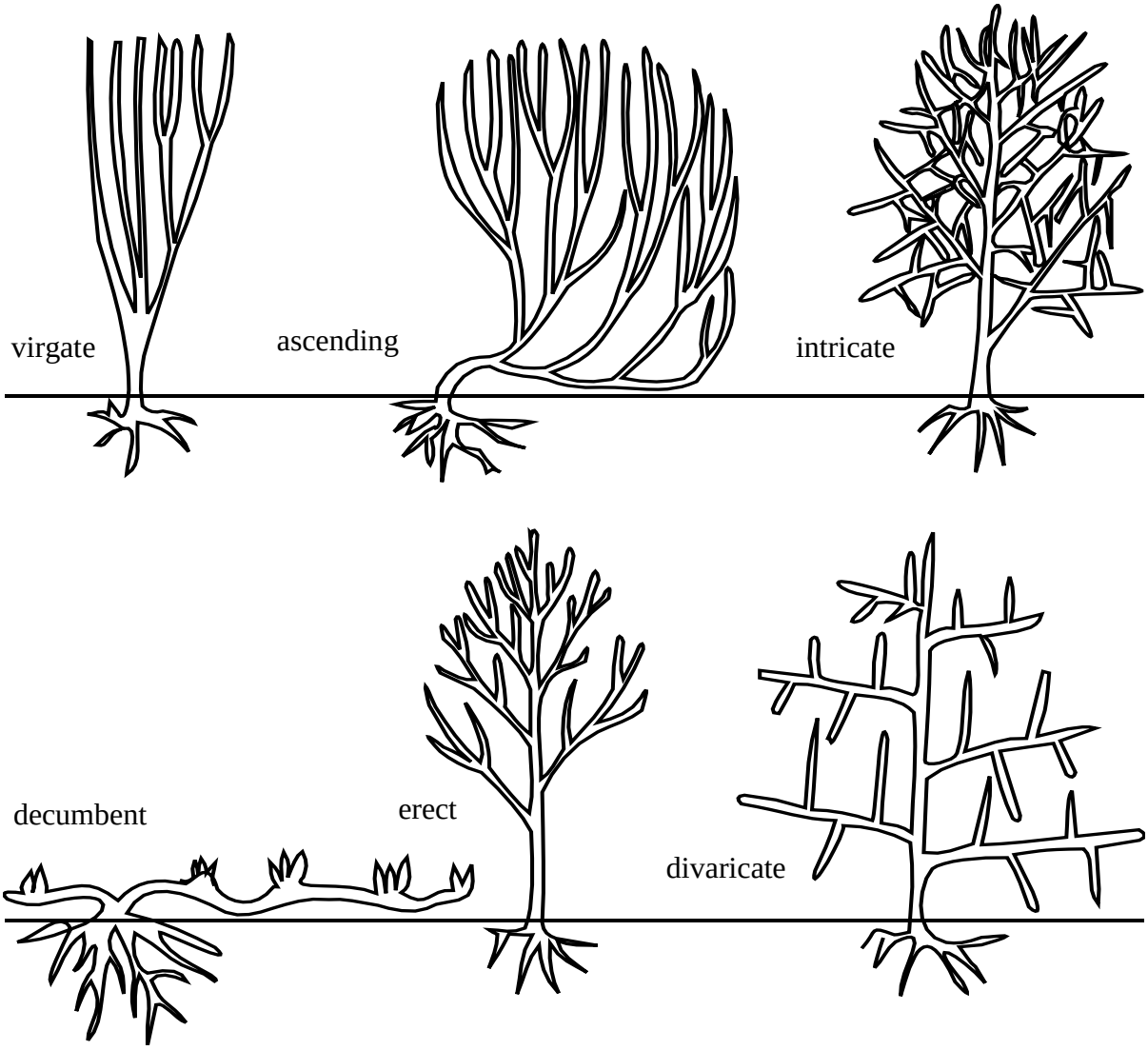



**Fig. 4.1:** A line illustration of the basic habits and branching patterns observed in *Thesium*

## 4.4 SPECIES TREATMENTS

### 4.4.1 *Thesium aspermontanum* Zhigila, Verboom & Muasya *sp. nov.* (Fig. 4.3)

*Type.* – South Africa. WESTERN CAPE: **3319 (Worcester):** Skurweberg Mountain (-AD), elev. 1131 m, 25 May 2017, *D.A. Zhigila 091* (holotype BOL; isotypes NBG, K).

*Diagnostic traits.* – *Thesium aspermontanum* shares traits with *T. subnudum* Sonder (1857: 360) namely finely sulcate stem transverse sections, scale-like leaves, staminal filaments exserted on the walls of perianth lobes, and ovoid to globose fruits. However, the former can be distinguished from the latter and allied species (Table 1A) [*e.g. T. nautimontanum* M.A.García, Nickrent & Mucina in García et al. (2018: 41)] by its bifurcating branchlets in the apical portion, which end in corymbose inflorescences (vs virgate branchlets ending in elongated terminal spikes), the absence of perianth lobe apical trichomes (vs the presence of perianth lobe apical trichomes), distinctively maroon old florets and maroon to reddish glaucous fruits (vs brownish to maroon old florets and green fruits).

*Description.* – Heath-like perennial *shrub*, up to about 400 mm tall, taproot system simple, rhizome lacking. *Stem* woody, erect, moderately branched, 0.5–0.8 mm in diameter, terete longitudinally, green with spotted red or maroon plant surface. *Branches* 3–5, mainly at base, angled at 45°, branching pattern sympodial, branchlets dense at end of each branch usually at distal portion or apical two-thirds of plant, vegetative buds in branchlet axils. *Leaves* well-developed, but lax, not imbricate, lanceolate, 4–5 × 0.4–0.5 mm, adpressed to stems, basally decurrent, not fleshy, green, old dried leaves red, midrib inconspicuous, not keeled, margins entire, apex acute. *Inflorescences* corymbose, at end of each branchlet, old florets red to maroons with scars of pedicels, peduncle 6–10 mm long. *Bracts* 3–5, leaf-like, adnate to base of peduncles, lanceolate, 3–5 × 0.4–0.5 mm, margin entire, green grading to maroon upon drying, apically acute; bracteoles 3–4, bract-like but smaller, adpressed to pedicel, shorter than flower. *Flowers* patelliform, 5-merous, 2.5–3.0 × 2.0–2.5 mm, perianth lobes lanceolate, external gland between lobes inconspicuous, 1.0–1.2 × 0.5–0.8 mm, lobe apex not distinctly uncinate, acute, straight, not recurved, lobe apical trichomes absent, lobe margins without trichomes, entire, lobes internal colour white, external colour green; hypanthium tube not clearly marked, short to about 0.2 mm long, shorter than perianth lobe tube, but wider. *Stamens* equal to perianth lobes, ca. 0.1–0.2 mm long, staminal filaments exserted above stigmas at junction between lobe and hypanthium tubes, basal trichomes absent. *Style* length including stigma 0.2–0.3 mm, stigma sessile; placental column twisted. *Fruit* a nutlet, ovoid, 2.0–2.5 mm, green when young and turns to reddish maroon at maturity, glabrous, prominently 10-ribbed, reticulate vein conspicuous, elaiosome absent, persistent perianth lobes shorter than

fruit to almost absent.

*Distribution and habitat.* – *Thesium aspermontanum* is a high elevation species endemic to the Skurweberg Mountain in the Western Cape Province of South Africa (Fig. 2A solid circles). It occurs on mountain summits and steep sandstone mountain Fynbos slopes at 1000–1500 m above sea level (a.s.l.). It is only known from three populations of approximately 500 individuals each. The substrate is somewhat reddish to golden ferricrete and silica-like elements upon which the species probably mimics its overall colouration.

*Phenology.* – *Thesium aspermontanum* was collected in May with flowers and dry fruits.

*Etymology.* – The specific epithet '*aspermontanum*' is a Latin interpretation and adjectival form of the Afrikaans name for the fold of ancient mountains 'Skurweberg' (meaning 'rough mountain') where this species was first collected.

*Conservation status.* – Further explorations for possible populations of this species are needed. Currently, the known populations have an extent of occurrence (EOO) of 4.00 $km^2$ and the area of occupancy (AOO) of < 1.00 $km^2$. Hence, *T. aspermontanum* is preliminarily classified as Critically Endangered (CR) under Criterion B2 of the IUCN Red List guidelines (IUCN, 2017).

*Taxonomic notes.* – *Thesium aspermontanum* resolves into Hill's *Thesium* sect. *Imberbia* subsect. *Subglabra* Hill (1915: 11). It shares the short papillose perianth lobe margins, patelliform flowers, and tuft of trichomes attaching staminal filaments to the perianth lobes with other species in this section (Hill 1915, 1925). Molecular phylogenetic reconstruction (Zhigila et al., 2020; Chapter 2) places *T. aspermontanum* as sister to *T. strictum* Bergius (1767:73) and allies, a clade comprising Hill's *Thesium* sect. *Penicillata* Hill (1915: 20). Species in this clade are characterised by well-marked perianth tubes, the absence of apical trichomes on the perianth lobes [with the exception of *T. penicillatum* Hill (1915: 37) in which these trichomes are present], and perianth lobe apices not distinctly uncinate. *Thesium aspermontanum* is distinct from members of this clade in its sympodial branching pattern, persistent red to maroon old florets, and being endemic to the Skurweberg Mountain (vs virgate or intricate branching patterns, and usually caducous old florets in related species).

*Additional materials studied.* – South Africa. WESTERN CAPE: **3319 (Worcester):** on neck of Monas Rivier, Sneeuberg Mountain and Skurwerberg Mountain (-AD), elev. 1168 m, 25 May 2017, *Zhigila 93* (BOL!, K!, NBG!).

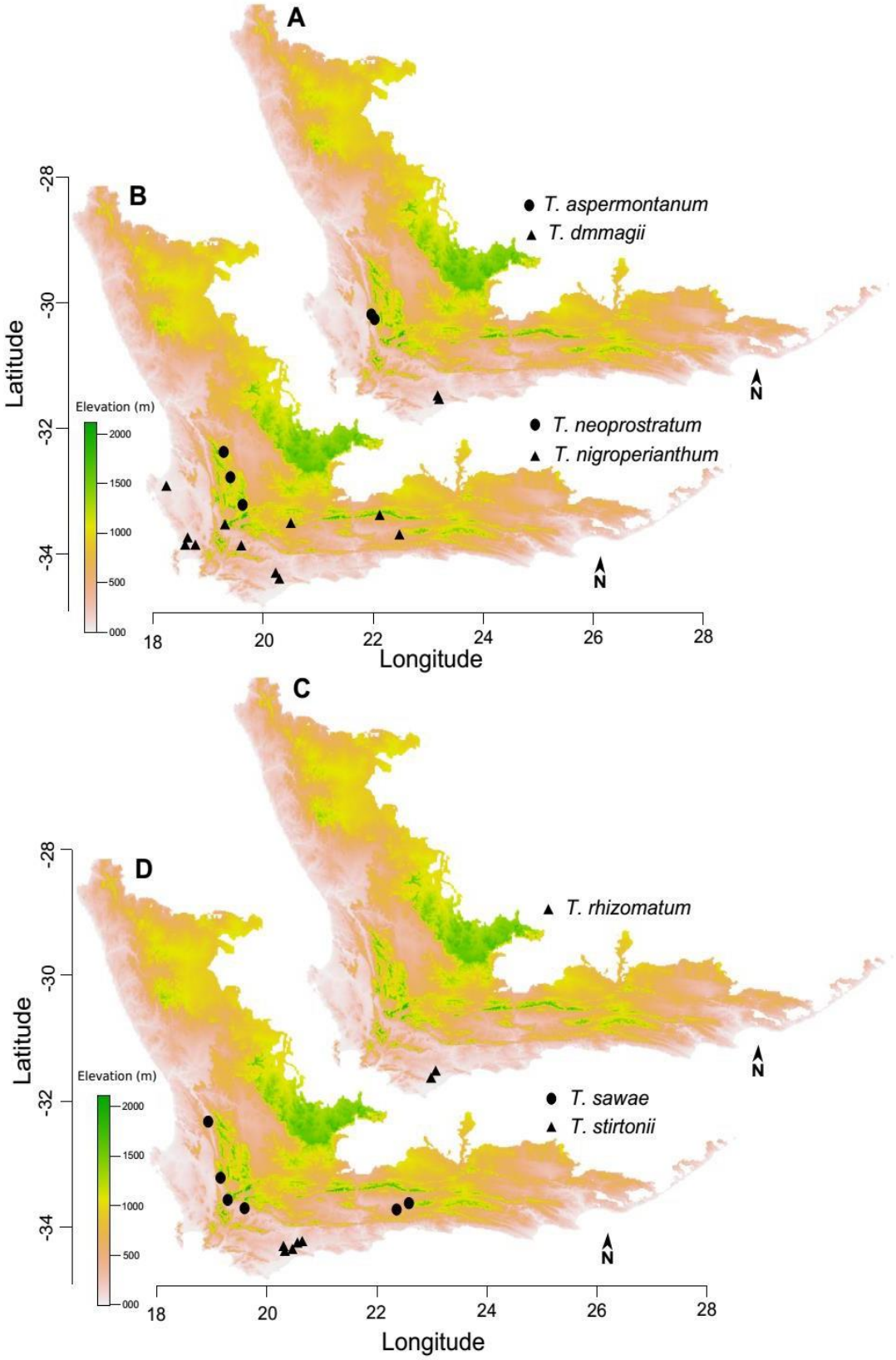



**Fig. 4.2:** Known geographical distribution of A) *T. aspermontanum* (circles) and *T. dmmagiae* (triangles). B) *T. nigroperianthum* (triangles) and *T. neoprostratum* (circles). C) *T. rhizomatum* (triangles). D) *Thesium stirtonii* (triangles) and *T. sawae* (circles).


**Fig. 4.3:** *Thesium aspermontanum.* A) Habit and habitat. B) Whole plant showing the sympodial branching pattern. C) Leafy twig. D) Twig showing a reddish old floret and a dried fruit in the axil of a branchlet. E) Fresh fruit. F) Longitudinal section of a fruit. G) Dried fruit.

**4.4.2** ***Thesium dmmagiae*** Zhigila, Verboom & Muasya ***sp. nov.*** (Fig. 4.4)

*Type.* – South Africa**.** WESTERN CAPE. **3420 (Bredasdorp):** on slopes above Vanderstelskraal Farm, Overberg (-AA), elev. 55 m, 11 September 2017, *D.A. Zhigila & A.M. Muasya 153* (holotype BOL; isotypes NBG, K).

*Diagnostic traits.* – *Thesium dmmagiae* keys out nearest to *T. frisea* Sond. (1857: 359) in existing keys (*e.g.* Hill, 1925). Both are slender, decumbent plants growing under larger shrubs, branching pattern decumbent, branches mainly at base, stem transverse section closely grooved, leaf tips apically subacute or acute, flowers clustered in terminal heads, flowers hypocrateriform, with a tuft of perianth lobe apical trichomes present. *Thesium dmmagiae* differs from *T. frisea* in having vegetative parts that are scabrid (vs glabrous), branches angled at almost 90° (vs about 45°), leaves being linear to lanceolate, terete or subterete to somewhat triangular and 4–10 mm long (vs linear, terete but not triangular and 10–15 mm long), flowers borne in panicles (vs spikes), and the flowers being polymerous (vs pentamerous) (Table 1B).

Specimens of *T. pubescens* De Candolle (1857b: 7) may be confused with *T. dmmagiae* based on their similar branching patterns and pubescent vegetative surfaces. *Thesium dmmagiae* can be distinguished by its sparsely scabrid vegetative parts, prostrate stems and smaller (4–10 mm), straight leaves (Table 1B) [vs the pubescent vegetative parts, erect stems and larger (10–25 mm) recurved leaves of *T. pubescens*].

*Description.* – Perennial undershrub, growing under bigger shrubs, 150–200 mm long, with lignified rootstock, and lacking a rhizome. *Stem* woody, prostrate, much-branched, 3–10 mm in diameter, with conspicuous longitudinal grooves, green, plant surface covered with short scabrid structures. *Branches* 5–15, mainly from base, arising off basal stolon, angled at 45°–90°, branching pattern decumbent, vegetative shoots in leaf axils. *Leaves* well-developed, adpressed to stem, not imbricate, dense on middle and apical parts of stem, linear to lanceolate, somewhat triangular to terete, 4–10 × 0.5–2.0 mm, basally decurrent, somewhat fleshy, midrib not prominent, margins entire, not cartilaginous, straight or convex, apices and margins brownish, apically subacute or acute. *Inflorescences* panicle of cymules, arranged in clusters of 8–12 flowers as cymose or globose terminal head, borne on peduncle 1–2 mm long, subtended by bracts and bracteoles. *Bracts* 2, leaf-like, adpressed to the peduncle, lanceolate, 1.5–3.0 × 0.5–2.5 mm, margins entire, apex acute, darkened; bracteoles 2, bract-like but smaller and narrower, adpressed to pedicel, shorter than flower. *Flowers* hypocrateriform, 4- to 6-merous (generally 5-merous), 3.0–4.5 × 0.5–1.5 mm, perianth lobe shape lanceolate, external gland between lobes absent, ca. 4–5 × 2–4 mm, lobe apex not distinctly uncinate, acute,

straight, with dense perianth lobe apical trichomes, lobe margin entire, internal colour of lobes white, external colour green at base grading to brown apically; hypanthium tube conspicuous, ca. 0.5 mm long, longer than perianth tube. *Stamens* equal to perianth lobes in merosity, 0.2–0.3 mm long, staminal filaments exserted above stigma, downwardly-directed basal trichomes present. *Style* length including stigma 0.1–0.2 mm, stigma sub-sessile; placental column not clearly visible. *Fruit* a nutlet, globose to ellipsoid, 3–4 × 2–3 mm, greenish brown, conspicuously 10-ribbed, clearly reticulate between ribs, elaiosome absent, persistent perianth lobes equal to or shorter than fruit.

*Distribution and habitat.* – *Thesium dmmagiae* is endemic to the Western Cape Province of South Africa where it is found in the Bredasdorp District. This species is locally restricted to the Eastern Rûens Shale Renosterveld and to an ecotone of shale and limestone substrates (Fig. 2C triangles) where it co-occurs with *T. rhizomatum* at 50–110 m above sea level.

*Phenology.* – Flowering and fruiting from July to December.

*Etymology.* – The specific epithet '*dmmagiae*' is named in honour of the first author's wife Dmmagi Daniel (1989–) for her immense support while he was in South Africa for *Thesium* studies.

*Conservation status.* – *Thesium dmmagiae* has a small distribution range (EOO = 0.093 $km^2$, AOO = 12.0 $km^2$) in areas exposed to detrimental and frequent bush fires and continuing anthropogenic pressures (*e.g.* agricultural activities). Hence, the species is vulnerable to even a single threat event that may cause its extinction or drastically reduce its numbers. Given that the few known populations are found only at slopes above the Vanderstelskraal farm and more information on its geographical range is required, we consider it Data Deficient (DD) based on the criteria given in the IUCN Red List guidelines (IUCN, 2017).

*Taxonomic notes.* – *Thesium dmmagiae* fits well into Hill's *Thesium* sect. *Annulata* Hill (1915: 20), which is characterised by a tuft of trichomes at the apex of the perianth lobes, and a set of downwardly-directed trichomes at the base of each staminal filament. However, *T. dmmagiae* differs in its scabrid surface and decumbent habit, traits absent in other species of this section (Table 1B).

*Additional materials studied.* – South Africa**.** WESTERN CAPE. **3420 (Bredasdorp):** on hill slopes above Vanderstelskraal farm, Overberg (-AA), elev. 150 m, 24 August 2018, *Zhigila & Muasya 254* (BOL!, NBG!, K!); between Caledon and Napier, Oct 1940, *Esterhuysen 5208* (BOL!); on limestone above Vanderstelskraal private farm, elev. 236 m, *Zhigila 281* (BOL!, NBG!).


**Fig. 4.4**: *Thesium dmmagiae*. A) Habit and habitat. B) Branching pattern and flower placement. C and D) Flowering shoots. E) Scabrid plant plant surface, terete or subterete to triangular leaves with brownish tips. F and G) Aerial view of two flowers, showing the differences in flower merousity and the tufts of trichomes on the lobe apices. H and I) Longitudinal section of a flower.

**4.4.3** ***Thesium neoprostratum*** Zhigila, Verboom & Muasya ***sp. nov.*** (Fig. 4.5)

*Type.* – South Africa. WESTERN CAPE: **3219 (Wuppertal):** Pakhuis Pass to Heuningvlei jeep track, Cederberg Wilderness (-AA), elev. 961 m, 23 May 2017, *D.A. Zhigila 081* (holotype BOL; isotypes NBG, K).

*Diagnostic traits.* – *Thesium neoprostratum* is similar to *T. prostratum* Hill (1915: 38) in that both plants are decumbent undershrubs with stems 200–250 mm long, the stems are terete to subterete in transverse section, and the plants are multicoloured (green, golden-yellow, red and maroon) in overall appearance, with branchlets and leaves yellowish green, old leaves and florets red to maroon, and tufts of vegetative buds typically in the branchlet axils. However, *T. neoprostratum* has hirsute vegetative surfaces, leaves 4–7 mm long with ciliate margins, and fruits that are longitudinally 5-ribbed and faintly reticulate (Table 1C), while *T. prostratum* has glabrous vegetative surfaces, leaves 5–10 mm long with entire margins, and fruits that are longitudinally 10-ribbed and conspicuously reticulate.

*Description.* – Perennial shrublet, straggling under bigger shrubs, 200–250 mm long, slender fibrous rootstock, and lacking a rhizome. *Stem* herbaceous, prostrate, much-branched, 0.8–1.2 mm in diameter, conspicuously grooved longitudinally, reddish brown to yellowish green, plant surface comprised of hispid structures. *Branches* 5–8, distributed sparingly along entire stem, angled to about 45°, branching pattern decumbent, vegetative buds in branchlet axils. *Leaves* well-developed, adpressed to stem, not imbricate, linear to acicular, 4–7 × 0.4–0.6 mm, basally decurrent, not fleshy, midrib inconspicuous, not keeled, apex acute, yellowish green, old dried leaves red, margins not distinct as leaves are terete, margin green, yellowish or red, apically acute. *Inflorescences* simple cymes, in a small cluster of 2–3 flowers held at terminal or subterminal end of each branchlet, peduncle 3–4 mm long. *Bracts* 4, leaf-like, adnate to base of peduncles, linear to lanceolate, 2–3 × 0.3–0.4 mm, margin ciliated with short hispid trichomes, apex acute to acuminate, old florets red or brown to maroon, flowers are almost completely hidden by bracts and bracteoles; bracteoles 4, bract-like, but smaller, adpressed to the pedicel, longer than flower. *Flowers* hypocrateriform, 5-merous, 2.0–2.5 × 0.5–1.0 mm, perianth lobes linear to lanceolate, external gland between lobes inconspicuous, 0.5–1.0 × 0.2–0.4 mm, lobe apex slightly uncinate, acute, straight, obtuse, not recurved, perianth lobe apical trichomes present, lobe margins with dense trichomes, entire, lobes internal colour white, external colour green; hypanthium tube conspicuous, up to about 0.5 mm long, longer than perianth lobe tube, wider at base. *Stamen* equal to perianth lobes in merosity, 0.2–0.4 mm, staminal filaments inserted, but longer than stigma, downwardly-directed basal

trichomes absent. *Style* length together with stigma 0.1–0.2 mm, stigma sessile; placental column twisted. *Fruit* a nutlet, ovoid to subglobose, 2.0–2.2 × 0.8–2.0 mm, green, longitudinally 5-ribbed, reticulate vein not prominent, elaiosome short to totally absent, persistent perianth lobes longer than fruit.

*Distribution and habitat.* – *Thesium neoprostratum* is endemic to the Western Cape Province of South Africa where it is distributed from Pakhuis Pass in the north to the Sneeuberg Mountains in the south and westward toward the Skurweberg Mountain flanks (Fig. 2B solid circles). The species has been collected from three relatively proximal sites with highest density observed at the Skurweberg Mountain summits. The tendency of this species to occur straggling under bushes renders it mostly unnoticed. It grows on rocky sandstone mountain Fynbos at 900–1200 m above sea level.

*Phenology*. – *Thesium neoprostratum* was collected in flower in May.

*Etymology*. – The specific epithet '*neoprostratum*' is derived from the Latin preposition '*neo*' meaning 'near' or 'close to' and an adjective '*prostrata'*, meaning prostrate, thereby depicting the resemblance of the new species to *T. prostratum*.

*Conservation status.* – The Sneeuberg and Skurweberg localities of this species are characterised by rugged landscapes surrounded by private lands, while the Pakhuis Pass (type locality) is under the protection of the Cape Nature as part of the Cederberg Wilderness Area. These areas are not under any unmitigated threats. However, Fynbos vegetation is often under frequent fire regimes that have negative post-fire regeneration consequences on reseeder species such as *T. neoprostratum*. Although more exploration is required to determine the conservation status of this taxon, its three known localities gives an estimated EOO of 1390.00 $km^2$ and AOO of 20.00 $km^2$ that falls under the Endangered (EN) category in the IUCN Red List guidelines (IUCN, 2017).

*Taxonomic notes.* – *Thesium neoprostratum* appears best placed in *Thesium* sect. *Annulata* Hill (1915: 20) or the leafy clade (sensu Moore et al., 2010) or the subgenus *Frisea* (Zhigila et al., 2020), because the leaves are well-developed and dense, the perianth lobes have apical trichomes, and the anthers are attached to the walls of perianth lobes by a bunch of trichomes, but lack downward facing trichomes that are typical of species in *T.* sect. *Annulata* (Hill 1915, 1925). Within this section, a molecular phylogenetic tree (Zhigila et al., 2020; Chapter 2) placed it as sister to *T. selagineum* De Candolle (1857b: 3).

*Additional materials studied.* – South Africa. WESTERN CAPE: **3219 (Wuppertal):** along main road, Op-die-Berg, Kouebokkeveld, S of Skurweberg Mountain (-AB), elev. 1005

m, 24 May 2017, *Zhigila 92* (BOL!, NBG!, K!); on neck of Monas River, Sneeuberg Mountain (-AD), elev. 1168 m, 25 May 2017, *Zhigila 86* (BOL!, NBG!, K!).

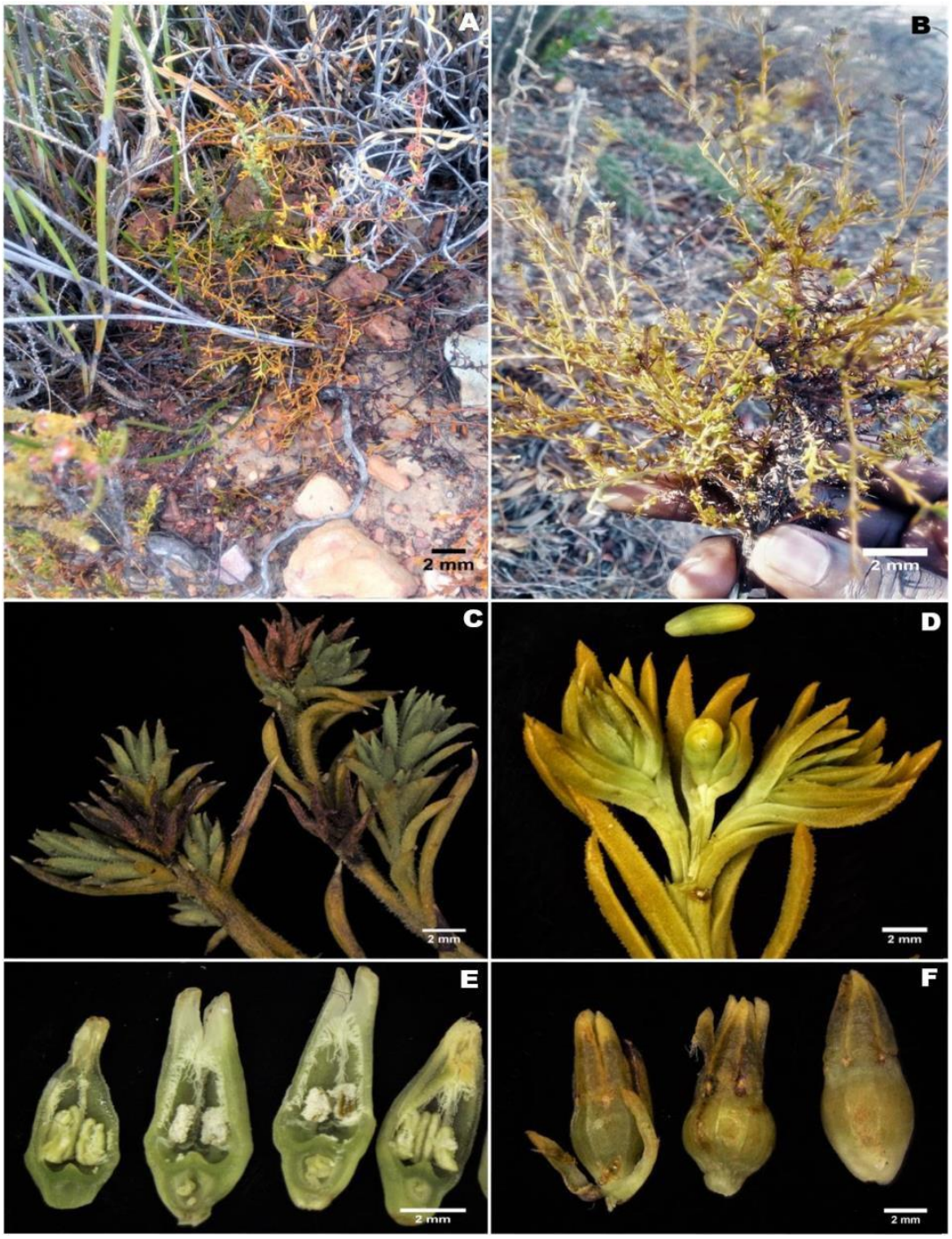



**Fig. 4.5:** *Thesium neoprostratum.* A) Straggling habit and the typical habitat. B) A branchlet twig. C) Close-up view of a branch showing the scabrid plant surface, green and reddish old leaves and old florets. D) An exposed budding flower in terminal head inflorescence. E) Longitudinal section of two flowers showing the twisted placental columns, hypanthium tubes that are shorter than the perianth lobes, sessile stigmas and exserted anthers. F) Fruits with faint longitudinal ribs and reticulate veins.

**4.4.4** ***Thesium nigroperianthum*** Zhigila, Verboom & Muasya ***sp. nov.*** (Fig. 4.6)

*Type.*– South Africa. WESTERN CAPE. **3420 (Bredasdorp)**: on slopes above Vanderstelskraal farm, Overberg, (-AA), elev. 217 m, 12 September 2017, *D.A. Zhigila & A.M. Muasya 151* (holotype, BOL; isotypes, NBG, K).

*Diagnostic traits.* – *Thesium nigroperianthum* shares some traits with *T. nigromontanum* Sonder (1857: 361). Both species have dense basal branches, blackened perianth lobe apices, conspicuous external glands between perianth lobes (Table 2A), and similar general floral arrangement (*e.g.* corymbose flower heads). *Thesium nigroperianthum*, however, differs from *T. nigromontanum* in its decumbent (vs erect) growth form, rough white spotted (vs smooth and brown) stems, and highly reduced, scale-like leaves (vs linear basal and lanceolate apical leaves) that are uniformly distributed along the branch lengths.

*Thesium nigroperianthum* is also similar to *T. stirtonii* in its woody rootstock and perennial woody stems, which are covered with rough spotted white structures, branching mainly at basal portions, scale-like leaves, paniculate inflorescences, patelliform flowers, and the absence of perianth lobe apical trichomes. *Thesium nigroperianthum*, however, differs from *T. stirtonii* in its perianth lobes being black (vs cream to green) on the outside, the black (vs cream to green) persistent perianth lobes on the fruits, and clearly grooved (vs slightly grooved) stems. *Thesium nigroperianthum* is furthermore restricted to shale and limestone substrate, or ecotones between these two substrates (vs specialization on quartz-silcrete outcrops and sandstone substrates).

*Description.* – Heath-like or growing under bigger shrubs, perennial shrub, about 200 mm long, taproot system simple, rhizome lacking. *Stem* woody, prostrate or suberect, moderately branched, 4–5 mm in diameter, slightly grooved longitudinally, green or brown with rough spotted white patches. *Branches* 5–10, mainly from the base, arising off basal stolon, angled from >45° to <90°, branching pattern divaricate or intricate, two types of branchlets, flowering and non-flowering, non-flowering branches grading to attenuate apex. *Leaves* scale-like, adpressed to branchlets, lax at base, imbricate at apex, ovate to triangular, 1.0–1.5 × 0.3–0.4 mm, basally decurrent, wider toward base, midrib inconspicuous, not keeled, green at base to about half the leaf length grading to brownish to maroon towards tip, margin papery and cartilaginous, serrulate, apices and margins maroon, apically acute to subacute. *Inflorescences* paniculate, flowers clustered 5–8 in corymbose terminal heads, on short peduncle (0.2–0.3 mm). *Bracts* 2, scale-like, base fusion slightly adnate to base of peduncle, lanceolate to ovate, 2.0–2.5 × 0.3–0.4 mm, margin entire, apex acute to acuminate, green to

brown or maroon; bracteoles bract-like, but smaller, adpressed to pedicel, shorter than flowers. *Flowers* patelliform, mostly 5-merous, but 6-merous do also occur, 2.0–2.5 × 1.5–2.0 mm, perianth lobes lanceolate to triangular, external gland conspicuously elongated between perianth lobes, 1.5–2.5 × 1.0–1.5 mm, lobe apex slightly uncinate, obtuse, straight, seldom recurved, perianth lobe apical trichomes absent, lobe margins with few minute structures forming denticulate edges, lobes internal colour white, external colour black or darkened; hypanthium tube clearly marked, short to about 0.2 mm long, tube length equal or shorter than perianth lobe tube, but wider. *Stamens* equal flower merosity, 0.2–0.3 mm long, staminal filaments exserted above stigmas, downwardly-directed basal trichomes absent. *Style* together with stigma 0.3–0.5 mm long; placental column twisted. *Fruit* a nutlet, ovoid to subglobose, 2.5–3.0 × 1.5–2.5 mm, green to creamy green, glabrous with 10 faintly longitudinal ribs, reticulate vein not prominent, elaiosome absent, blackish persistent perianth lobes shorter than fruit.

*Distribution and habitat.* – *Thesium nigroperianthum* occurs widely throughout the Western Cape, South Africa, from the west coast and Cape Flats in the west into the Karoo areas and toward Robertson in the east (Fig. 2B triangles). This species occurs on shale and alluvial soils, and is found in mountain Renosterveld, dry mountain Fynbos and shale-limestone ecotone vegetations. It usually occurs at elevations of 170–300 m above sea level.

*Phenology.* – Flowering and fruiting from July to December.

*Etymology.* – The specific epithet '*nigroperianthum*' is a compound word derived from two Greek terms '*nigro*' meaning 'black' and '*perianth*' meaning 'outermost two whorls of a flower', alluding to the black perianth lobe apices of the taxon, which also persist on the fruits.

*Conservation status.* – This taxon has a wide, albeit scattered, distribution across the GCFR. Some of its populations are on private farms or nature reserves, without any immediate threats, besides the unwarranted frequent bush fires that characterise the GCFR. GeoCAT estimates of the EOO and AOO were 59 053.74 km$^2$ and AOO 56.0 km$^2$, respectively. These estimates fall under the Least Concern (LC) category of the IUCN Red List guidelines (IUCN 2017).

*Taxonomic notes.* – *Thesium nigroperianthum* fits into *Thesium* sect. *Imberbia* subsect. *Subglabra*. This subsection, together with subsect. *Fimbriata* Hill (1915: 14), corresponds with *T.* sect. *Discothesium* De Candolle (1857a: 661), which Hill (1925) submerged into *T.* sect. *Imberbia* along with sect. *Euthesium* De Candolle (1857a: 639) and sect. *Aetheothesium* De Candolle (1857a: 660). Species in *T.* sect. *Imberbia* share characters such as glabrous perianth lobe apices, papillose (subsect. *Subglabra*) or lacinulate (subsect. *Fimbriata*) perianth lobe

margins, distinctly uncinate perianth lobes, and patelliform flowers (Hill, 1915).

*Additional materials studied.* – South Africa**.** WESTERN CAPE: **3218 (Clanwilliam):** Langeklip 47, 8 km S of St. Helena, Stemmet's kop area (-DA), elev. 210 m, 3 September 2008, *Helme 5639* (NBG!, STE!). **3318 (Cape Town):** flats 5 miles SE of station, Cape Town, 21 August 1972, *Oliver 3788* (K!). Blackheath Fynbos, Mont Rochelle Nature Reserve, above Franschhoek (-DC), elev. 5 m, 21 August 1972, *Oliver 3788* (K!, NBG!, STE!); Blackheath Fynbos, Rochelle Nature Reserve, above Franschhoek (-CC), elev. 50 m, 10 April 1957, *Levyns 10674* (BOL!); Sandberg SW of the town Robertson District (-DA), *Oliver 10508* (NBG!, K!). **3320 (Montagu):** above farm Anysberg (-CB), elev. 820 m, 1 August 1987, *Brown 517* (STE!). **3322 (Oudtshoorn):** on shale nutrient-rich soil, base of Kamannasieberg at Rietvlei, along road to Mannetjiesberg (-DB), elev. 800 m, 10 November 2006, *Verboom 1153* (BOL!, NBG!); Korlandskloof, shaley playground, Bredasdorp, elev. 132 m, 7 September 1975, *Oliver 6015* (STE!). **3420 (Bredasdorp):** De Hoop, limestone ridge (–AD), elev. 15 m, 20 June 2008, *Moore 68* (BOL!); in the valley with alluvial soil between two limestone caps above Vanderstelskraal farm (-AA), elev. 282 m, *Zhigila 282* (BOL!, NBG!).

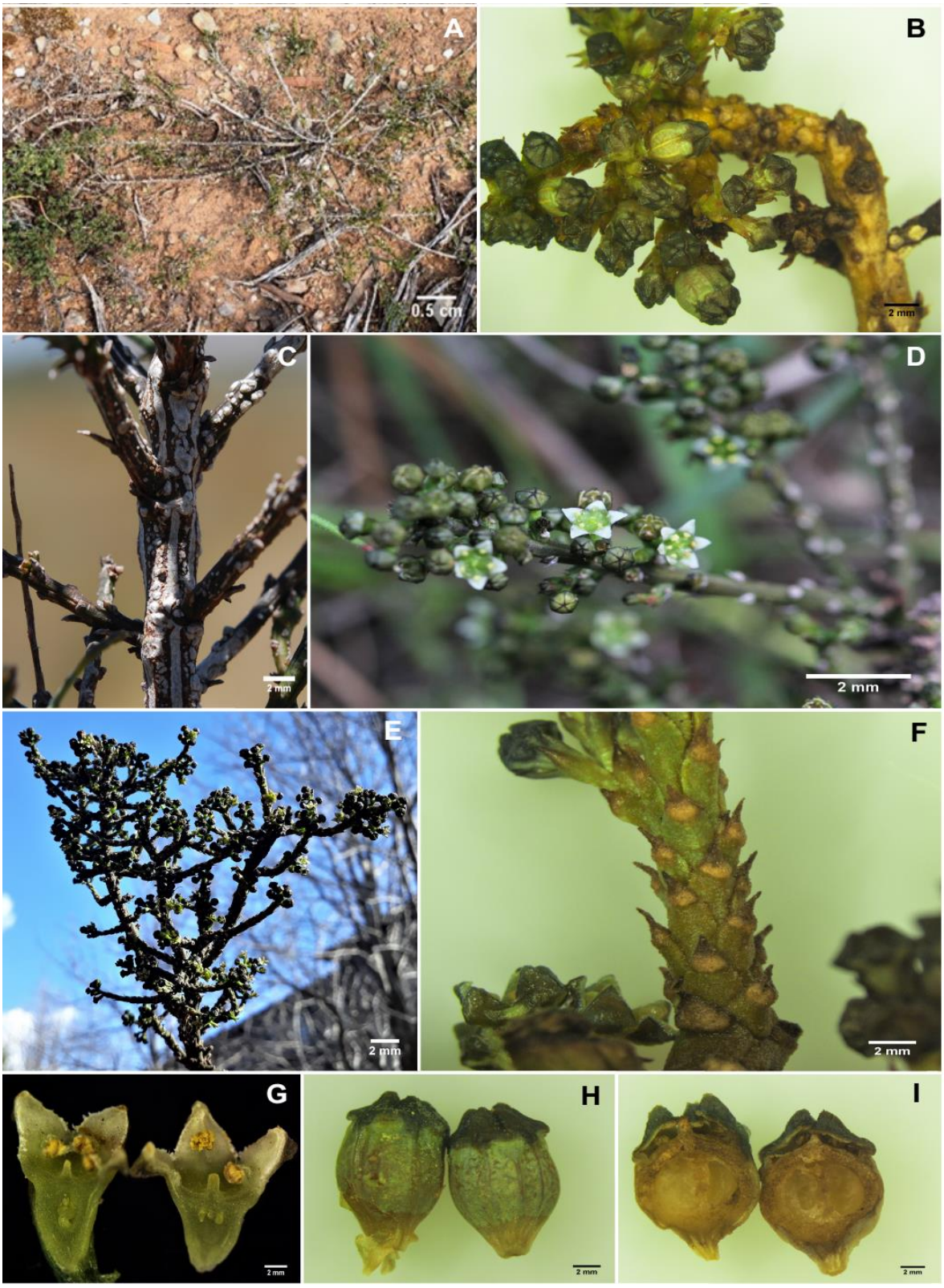



**Fig. 4.6:** *Thesium nigroperianthum.* A) Decumbent habit and shale-like substrate. B) Fruiting shoot. C) Branching angles and plant surface. D) Flowering shoots (photo by O.E. Curtis). E) Aerial view of the intricate branching pattern. F) Scale-like leaves, fleshy at the base and attenuate toward the tips. G) Longitudinal section of a flower. H) Fruit with short persistent blackish perianth lobes. I) Fruit longitudinal section.

**4.4.5** ***Thesium rhizomatum*** Zhigila, Verboom & Muasya ***sp. nov***. (Fig. 4.7)

*Type.* – South Africa. WESTERN CAPE. **3420 (Bredasdorp):** on hill slopes above Vanderstelskraal farm, Overberg (-AA), elev. 109 m, 11 September 2017, *D.A. Zhigila & A.M. Muasya 152* (holotype BOL; isotypes NBG, K).

*Diagnostic traits. – Thesium rhizomatum* is similar to *T. minus* (Hill, 1915b: 98) J.C.Manning & F.Forest in Forest & Manning (2013: 25) as both have long subterranean stems (rhizomes), which are usually more robust than the herbaceous annual aerial stems, small stature, 40–80 mm tall, virgate branching patterns, glabrous plant surfaces, well-developed linear leaves, patelliform flowers, and ovoid, 10-ribbed fruits. However, *T. rhizomatum* is distinguishable from *T. minus* in being a hermaphrodite (vs dioecious), in having corymbose inflorescences at the end of each branchlet (vs flowers in spikes arranged along the branch length in each leaf axil), bracts and bracteoles that are shorter than or equal to the flower (vs much longer than the flowers), five stamens (vs four stamens), and papillose perianth lobe margins (vs entire perianth lobe margins) (Table 2B).

*Description. – Herb* with annual aerial stems and perennial subterranean parts, 40–80 mm tall, with fibrous root system, rhizomes present, 100–250 mm long. *Stems* herbaceous, aerial shoots erect, branches few, 2–5 mm in diameter, conspicuously grooved longitudinally, green, glabrous. *Branches* 3–6, at distal portion, angled at about 45°, branching pattern virgate, branchlet shoots arise in axil of each leaf. *Leaves* well-developed, adpressed to stem, densely arranged on whole shoot, but not imbricate, linear, 3–6 × 1–3 mm, thick to slightly succulent, basally decurrent, midrib not raised as leaf is slightly terete or somewhat triangular, edges entire, not cartilaginous, flapped backward, apices and margins green, apex acute. *Inflorescences* corymbose, with flowers crowded in groups of 5–10 at branch terminals, peduncle 1.5–2.5 mm long. *Bracts* 2, leaf-like, adpressed to peduncle, linear to lanceolate, 2–5 × 0.5–1.5 mm, margins entire, greenish, grading to brownish toward apex, apically acute, bracteoles 2, bract-like, but smaller, adpressed to pedicel, shorter than or equal to flower length, seldom longer. *Flowers* patelliform, 5–8 × 4–6 mm, 5-merous, perianth lobes triangular, external glands between lobes inconspicuous, about 3 × 4 mm, lobe apex not distinctly uncinate, obtuse, usually straight, but becomes recurved with age, perianth lobe apical trichomes absent, lobe margins with hirsute papillae forming ciliated edges, lobes internal colour white, external colour creamy green; hypanthium tube short, 0.3–0.4 mm long, tube length shorter than perianth tube, but wider. *Stamens* equal to perianth lobes in merosity, short, 0.2–0.3 mm long, staminal filaments exserted above stigmas, downwardly-directed basal

trichomes absent. *Style* short or sub-sessile, 0.2–0.3 mm; placental column straight. *Fruit* a nutlet, ovoid, elaiosome absent, 1.0–1.5 × 2.0–3.5 mm, greenish, longitudinally distinct and reticulated ribs up to 10 with anastomosing veins, persistent perianth lobes shorter than fruit.

*Distribution and habitat.* – *Thesium rhizomatum* is endemic to the Western Cape Province of South Africa. It occurs in shale Renosterveld, as well as the ecotone of the Shale Fynbos and Limestone Fynbos vegetation of the Overberg, at 100–150 m above sea level. (Fig. 2C triangles). It was found in vegetation that burnt more than 5 years ago, and also in relatively recently burned (2 years ago) veld. Three populations of juveniles with about 50 individuals each were found growing in a typical Renosterveld vegetation on nutrient-rich shale soils. It also appears to be resprouting from its long subterranean rhizomes after fire.

*Phenology.* – Flowering from July to December.

*Etymology.* – The specific epithet '*rhizomatum*' is derived from the Greek '*rhízōma*' = "mass of roots" and refers to the rhizomatous subterranean parts, which are much longer (100–250 mm) than the aerial parts (40–80 mm) of this species.

*Conservation status.* – This taxon is locally known from the upper slopes of Vanderstelskraal Farm. This locality is included in one of the Renosterveld patches considered to be Critically Endangered due to excessive land clearing for farming activities, overgrazing, and frequent bush fires (Raimondo et al., 2009). Given that *T. rhizomatum* is a habitat specialist known only from this area, whose EOO was identified as < 1.00 $km^2$ and the AOO of < 4.00 $km^2$, we suggest that it be classified as Critically Endangered (CR) under Criterion B1 as per the IUCN Red List guidelines (IUCN, 2017).

*Taxonomic notes.* – Although material of species in *Thesium* sect. *Imberbia* subsect. *Subglabra*, to which *T. rhizomatum* belongs, are rather heterogenous (Hill, 1925), *T. rhizomatum* differs from other GCFR species in this section in a number of striking traits. These include the small size (40–80 mm tall), perennial subterranean rhizomes, and herbaceous annual shoots. Also, while most species in this section are characterized by conspicuous external glands anastomosing the perianth lobes, these glands are inconspicuous in *T. rhizomatum* (Table 2B).

*Additional materials studied.* – South Africa**.** WESTERN CAPE. **3420 (Bredasdorp):** on hill slopes above Vanderstelskraal farm, Overberg (-AA), elev. 110 m, 24 August 2018, *Zhigila & Muasya 253* (BOL!, NBG!, K!); toward the W limestone cap, above Vanderstelskraal farm, elev. 111 m, *Zhigila 280* (BOL!, NBG!).

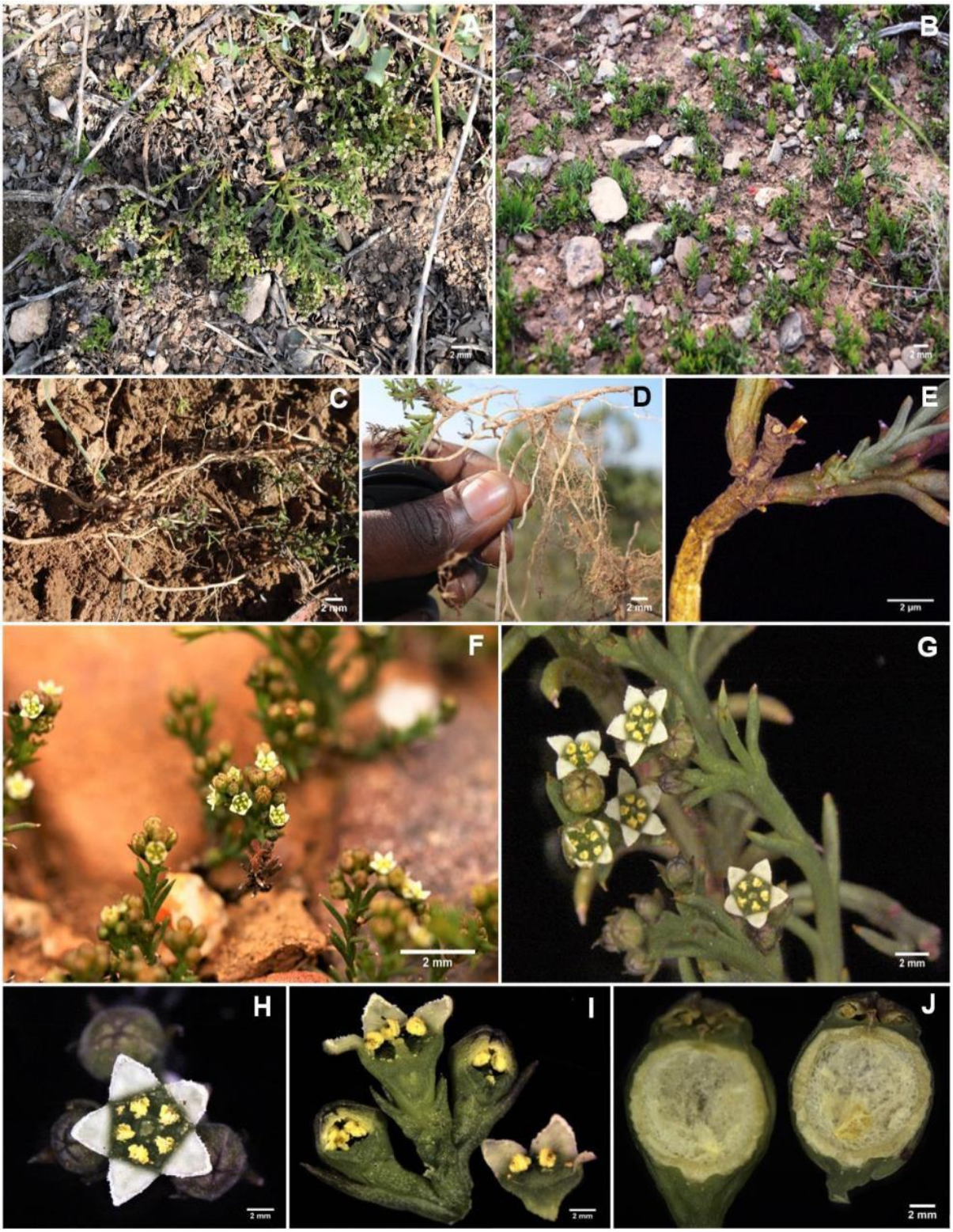



**Fig. 4.7:** *Thesium rhizomatum*. A) Habit of mature plants, as well as the typical habitat where this species occurs. B) A population of about 40 juveniles. C) Exposed subterranean rhizomes. D and E) Rhizomes with sprouting shoots. F and G) Flowering shoots. H) Aerial view of the patelliform flower showing distinctly uncinate perianth lobes and ciliate and margins. I) Longitudinal section of a flower displaying the placenta, exserted staminal filaments and style. J) Dissected fruit.

**4.4.6** ***Thesium sawae*** Zhigila, Verboom & Muasya ***nom. et stat. nov.*** (Fig. 4.8).

*Replaced synonym.* – *Thesium assimile* Sonder (1857: 360) var. *pallidum* Sonder (1857: 360). Homotypic synonym. – *Thesium carinatum* De Candolle (1857b: 7) var. *pallidum* (Sond.)Hill (1925: 193). Type: South Africa. WESTERN CAPE. **3319 (Worcester):** Worcester, near Waterfall (-CB), elev. 500 m, *C.F. Ecklon & C.L.P. Zeyher s.n.* (Lectotype designated here, S!; isolectotypes BOL!, K!).

*Diagnostic traits.* – *Thesium sawae* is superficially similar to *T. carinatum* De Candolle (1857b: 7) and *T. viridifolium* Levyns (1950: 74) in its linear subterete to somewhat triangular leaves, minutely ciliated leaf margins and the presence of apical trichomes on the perianth lobes. *Thesium sawae* differs from both *T. carinatum* and *T. viridifolium* in a combination of its decumbent or suberect habit, growing up to about 250 mm tall, intricate branching pattern (vs erect habits, both growing up to about 500 mm tall, usually virgate branching patterns), flowers in laxer heads, and yellowish to creamy white old florets (vs flowers compact on terminal or axillary branches, and coffee brown old florets).

*Description.* – Heath-like or growing under other bushes, perennial shrublet, 200–250 mm tall, with slender to woody-fibrous root system, rhizome lacking. *Stem* woody, decumbent or suberect, moderately branched, 0.8–1.5 mm in diameter, slightly grooved longitudinally, reddish brown or golden green to yellowish green, plant surface glabrous with scars of old leaves visible. *Branches* 5–8, distributed sparingly along entire stem, angled to about 45°, branching pattern intricate or divaricate, vegetative buds in branchlet axils. *Leaves* well-developed, adpressed to stem, not imbricate, linear, 7–10 × 0.8–1.0 mm, basally decurrent, somewhat fleshy, midrib and margin aspects not applicable as leaves are somewhat triangular with angle edges minutely ciliate and distinctly raised, margin yellowish green, apically acute. *Inflorescences* globose cymes, in axils of each branchlet or at end of each terminal lax heads, peduncle 2–3 mm long. *Bracts* 2, leaf-like, adnate to base of peduncles, linear to lanceolate, 3–5 × 0.4–0.5 mm, margin membranous, entire, apex acute, old florets white in axils of old creamy-white dried leaves; bracteoles 2, bract-like, but smaller, adpressed to pedicel, equal to or longer than flower. *Flowers* hypocrateriform, 5-merous, 3.5–4.0 × 1.0–1.5 mm, perianth lobes lanceolate, external glands between perianth lobes inconspicuous, 0.8–1.0 × 0.3–0.5 mm, lobe apex distinctly uncinate, acute, straight, not recurved, perianth lobe apical trichomes present, lobe margins with dense trichomes, entire, internal colour of lobes white, external colour golden green; hypanthium distinct, 0.4 mm long, longer than perianth lobes, wider at base. *Stamens* equal to perianth lobes in merosity, 0.2–0.4 mm long, staminal filament exserted

at base of perianth and above stigma, downwardly-directed basal trichomes absent. *Style* length including stigma 0.2–0.3 mm long, stigma sessile to subsessile; placental column twisted. *Fruit* a nutlet, ellipsoid-globose, to about 4 mm long, glabrous with 10 longitudinal ribs, reticulate veins faint, green to glossy, elaiosome short to absent, persistent perianth lobes longer than fruit.

*Distribution and habitat.* – *Thesium sawae* is a mountain Fynbos species geographically distributed from Pakhuis Pass in the north to the Piketberg Mountain in the southwest and then toward the southwest into the winter rainfall sandstone Fynbos areas of the Cape Peninsula, and eastward toward the central regions of Swartberg Pass and Prince Albert Division (Fig. 2D solid circles). It occurs strictly in sandstone mountain Fynbos at 200–1200 m above sea level.

*Phenology.* – Flowering from February to November.

*Etymology.* – The specific epithet '*sawae'* was assigned in honour of Prof. (Mrs) Fatima B.J. Sawa, a renowned Nigerian botanist, for her mentorship and support toward the first author's botanical career.

*Conservation status.* – *Thesium sawae* was found in abundance across its geographical range without any plausible threats. However, the AOO and the EOO were 15 445.704 $km^2$ and 96 000 $km^2$ , respectively, which gives it a regional conservation status of Vulnerable (VU) under Criterion D2 of the IUCN Red List guidelines (IUCN, 2017).

*Taxonomic notes.* – This species was described twice in 1857, first as *T. carinatum* by De Candolle (1857b: 2) and then as *T. assimile* by Sonder (1857: 360). Hill (1925) rightly applied *T. assimile* as a synonym of *T. carinatum*, as it is still treated. Hill (1925) also classified *T. assimile* var. *pallidum,* the replaced synonym of *T. sawae,* as a variety of *T. carinatum* based on its paler leaves (especially when dry) and laxer corymbose inflorescences than in *T. carinatum*. *Thesium carinatum* var. *pallidum* was subsequently applied as such by several collectors (*e.g.* herbarium sheets of *Lewis 22378, Bolus 2937* and *Burchell 296*). Following a critical study of the type specimen of *T. carinatum* var. *pallidum*, as well as materials of the taxon in its natural habitats and other herbarium specimens, we found significant traits that remained distinct enough to warrant an upgrade to specific rank. These characters include plant height to about 250 mm tall, decumbent or suberect habit, intricate branching pattern and creamy old florets (vs plant height to about 500 mm tall, erect habit, virgate branching pattern and old florets usually lacking, but blackish if present in *T. carinatum*). These distinguishing traits add to the paler leaves and laxer inflorescences (Table 1D) upon which Hill (1925) based his varietal status. The name *T. sawae* is here proposed as a *nomen novum* for this species, since the variety name '*pallidum*' is not available at species level and would result in an illegitimate

later homonym (Art. 6.11, Turland et al., 2018), given the older validly published name *T. pallidum* De Candolle (1857: 2).

*Thesium sawae* belongs to *Thesium* sect. *Barbata* Hill (1915: 15) or the leafy clade (sensu Moore et al., 2010) since the leaves are well-developed and densely distributed along the entire plant, the perianth lobe apices are covered with dense trichomes, and basal trichomes are lacking (Hill 1915; 1925).

*Additional materials studied.* – South Africa. WESTERN CAPE. **3219 (Wuppertal):** on jeep track to Eikeboom, toward Sneeuberg Mountain (-AC), elev. 1112 m, 24 May 2017, *Zhigila 85* (BOL!, K!, NBG!). **3318 (Cape Town):** Cape Town, September 1976, *Bolus 2939* (K!); Lion's Head (-CD), *Burchell 296* (K!). **3319 (Worcester):** Franschhoek Forest Reserve, 28 September 1935, *Lewis 22378* (K!); about 200 m from Bain's Kloof lodge, on trial path to Happy Valley, Limietberg Nature Reserve (-CC), elev. 562 m, 27 April 2017, *Zhigila 33* (BOL!, NBG!, K!); on footpath toward the river from Bain's Kloof lodge, Limietberg Nature Reserve (-CC), elev. 501 m, 27 April 2017, *Zhigila, D.A. 35* (BOL!, K!, NBG!); Sentech Yard, Jonaskorp (-CA), elev. 1590 m, 10 May 2017, *Zhigila 75* (BOL!, NBG!, K!). along jeep track, Pakhuis-Heuningvlei, Cederberg (-AA), elev. 983 m, 23 May 2017, *Zhigila 79* (BOL!, K!, NBG!);

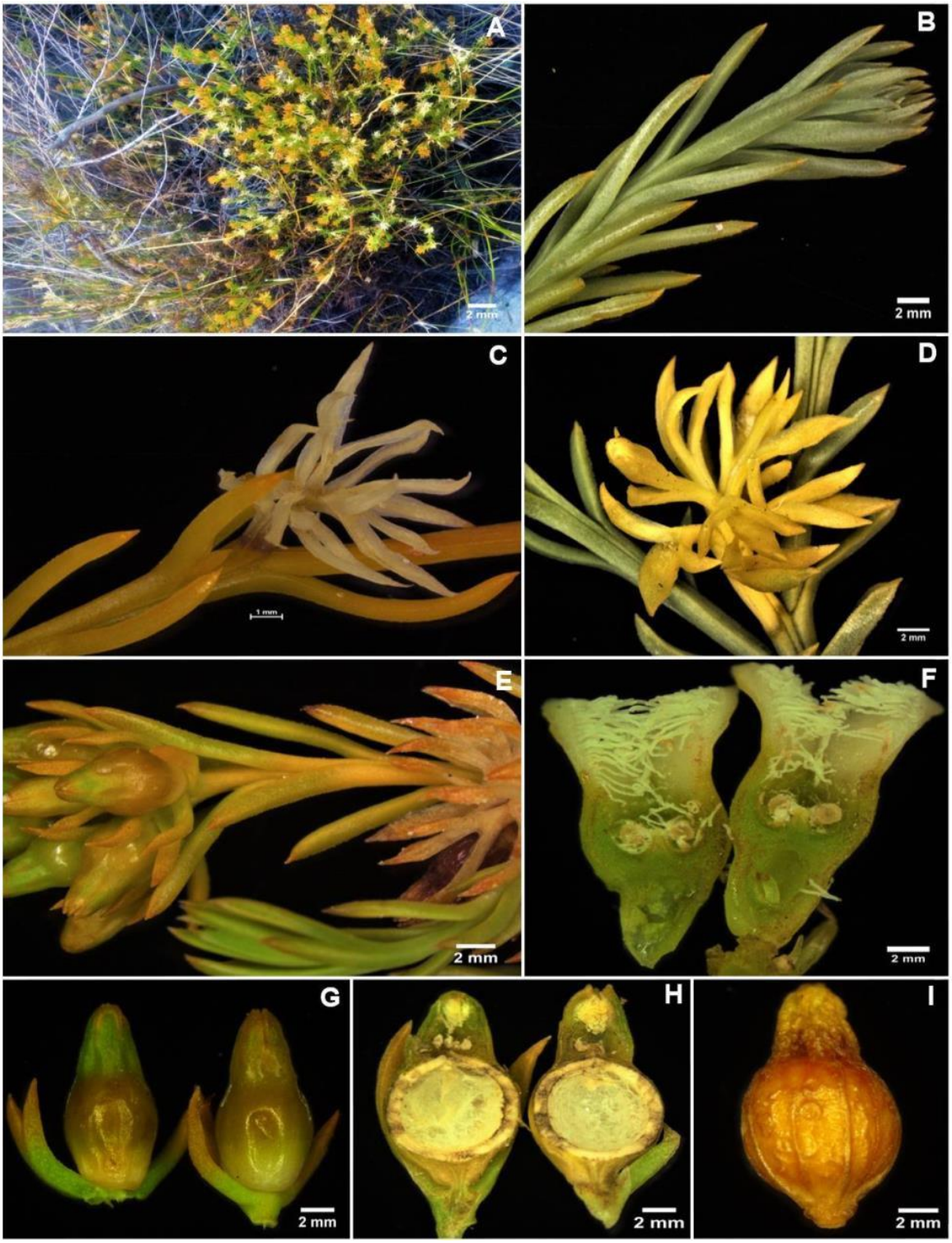



**Fig. 4.8:** *Thesium sawae.* A) Habit (elegant multi-coloured overall appearance) and typical habitat. B) Greenish leafy twig. C) Golden leafy branchlet with a cream old floret. D) Twig showing a yellowish immature floret in the axil of a branchlet. E) Fruiting branchlet. F) Flower longitudinal section showing the tuft of perianth lobe apical trichomes at the lobe apices. G) Fruits with inconspicuous longitudinal ribs and reticulate venation. H) Dissected fruit. I) Dried fruit.

**4.4.7** ***Thesium stirtonii*** Zhigila, Verboom & Muasya ***sp. nov.*** (Fig. 9)

*Type.* – South Africa. WESTERN CAPE. **3420 (Bredasdorp)**: Haarwegskloof Renosterveld Reserve, along trail paths in the reserve, on quartz patches, full sun and open canopies (-AA), elev. 278 m, 12 September 2017, *D.A. Zhigila & A.M. Muasya 148* (holotype BOL; isotypes NBG, K).

*Diagnostic traits.* – *Thesium stirtonii* is similar to *T. flexuosum* De Candolle (1857b: 6) in being a heath-like shrub, which is much-branched at the base with a virgate branching pattern, scale-like leaves, and bracts and bracteoles with acute tips. *Thesium stirtonii* differs in its compact, paniculate inflorescences that consist of 5- to 7-flowered terminal heads (vs lax, spicate inflorescences arranged along the branchlets), bracts and bracteoles that are green at the base and maroon toward the margins (vs bracts and bracteoles that are green at the base with white-edged membranous margins), flowers that are patelliform with recurved perianth lobes (vs the hypocrateriform flowers with straight perianth lobes), the lack of apical trichomes on the perianth lobe tips, and the long, conspicuous external glands between the perianth lobes (vs the presence of an apical tuft of trichomes on the perianth lobes, and inconspicuous external glands between the perianth lobes).

*Thesium stirtonii* can also be likened to *T. leptocaule* Sonder (1857: 362) as both species have a spotted stem plant surface and crowded inflorescences, but *T. stirtonii* differs from *T. leptocaule* in its decumbent or suberect habit, consistently scale-like leaves (vs erect habit and dimorphic leaves, linear at the base and grading to scale-like leaves towards the inflorescences), the presence of both flowering and non-flowering branchlets and conspicuous external glands between perianth lobes (vs flowering branchlets only and the absence of external glands between perianth lobes) (Table 2C).

*Description.* – Heath-like perennial shrub, 200–400 mm tall, taproot system simple, rhizome lacking. *Stems* woody, decumbent or suberect, much-branched, 3–5 mm in diameter, with conspicuous longitudinal grooves, brownish green with spotted and striped plant surface. *Branches* 5–15, mainly arising from basal stolon, angled at about 45°, branching pattern virgate, branchlets dimorphic (flowering and non-flowering), non-flowering branchlets attenuate toward apex. *Leaves* scale-like, adpressed to stem, imbricate (particularly on non-flowering branchlets), ovate to triangular, 1.5–4.0 × 1–2 mm, basally decurrent, broad, fleshy and green basally to about half the leaf length grading to brownish maroon toward tip and margins, apex acute to subacute, midrib inconspicuous, but slightly keeled, margin papery and cartilaginous, serrulate. *Inflorescences* paniculate, flowers in groups of 5–7 per flowering

shoot, peduncles very short or sessile, up to 0.7 mm long. *Bracts* 2, scale-like, adpressed to peduncle, ovate to triangular, 1–2 × 1.5–2.0 mm, margins cartilaginous, brownish to maroon, apically acute; bracteoles 2, bract-like, but smaller, adpressed to pedicel, shorter than flower. *Flowers* patelliform, generally 4- to 6-merous (rarely 7-merous), 5–8 × 3–5 mm, perianth lobes lanceolate to triangular, external glands conspicuously elongated between lobes, ca. 3.4 × 4.0 mm, lobe apex distinctly uncinate, obtuse, recurved and rarely straight, lobe apical trichomes absent, margins with minute papillae forming denticulate edges, lobes internal colour white with greenish patches, external colour green to brown or maroon, hypanthium conspicuous, ca. 0.5 mm long, shorter but wider than perianth lobes . *Stamens* equal to perianth lobes in merosity, ca. 0.4 mm long, staminal filaments exserted above stigmas, downwardly-directed basal trichomes absent. *Style* length including stigma ca. 0.3 mm long, placental column twisted. *Fruit* a nutlet, elliptic to subglobose, 2–5 × 2–3 mm, greenish, glabrous, with 10 longitudinal ribs and faint reticulate venation, elaiosome absent, persistent perianth shorter than fruit.

*Distribution and habitat.* – This species is endemic to the Western Cape Province of South Africa, where it occurs in typical Renosterveld scrub vegetation on silcrete, quartzite pebbles and shale soils of the Overberg, Bredasdorp District (Fig. 2D, solid triangles). Generally, it is found in exposed sunny sites, at elevations of 100–300 m above sea level.

*Phenology.* – Flowering and fruiting from July to December.

*Conservation status.* – *Thesium stirtonii* is locally common within its known distribution range in the natural Renosterveld and Fynbos vegetation fragments of the Overberg. Although some of these patches are within nature reserves and others are difficult to access due to rugged terrain, some populations are threatened by overgrazing (*T. stirtonii* was observed to be palatable to mammals), agricultural activities, and frequent bush fires. These areas are also listed among the Critically Endangered habitats in Raimondo et al. (2009). The extent of occurrence (EOO) was identified as 580.23 $km^2$ and the area of occupancy (AOO) as 60.00 $km^2$, which falls in the Endangered (EN) category under Criterion B2 of the IUCN Red List guidelines (IUCN, 2017).

*Etymology.* – The specific epithet '*stirtonii*' honours Professor Emeritus Charles H. Stirton (1946–) whose contributions have expanded our knowledge of the botany of *Thesium.* Out of love and for his sustained interest in the group, he collected 86 accessions of ca. 40 *Thesium* species among which four are new.

*Taxonomic notes.* – *Thesium stirtonii* has been misidentified as *T. nudicaule* Hill (1915: 35) (sensu *Helme, 1744; Lewis, 22378; Bolus, 2937; Burchell, 296*), as these two species are superficially similar in their scale-like leaves, conspicuous external glands between the perianth lobes, somewhat patelliform flowers, and darkened perianth lobe apices. However, a critical examination of the type specimen of *T. nudicaule* revealed some striking characters distinguishing it from *T. stirtonii*. *Thesium nudicaule* is a shrublet with an erect habit, spike-like or 3-flowered dichasial inflorescences, and black perianth apices (Hill, 1915; 1925; Table 2C), (vs shrubby, prostrate habit, paniculate inflorescences, and brown perianth apices in *T. stirtonii*). In the context of previous classification placements (Hill, 1915; 1925), *T. stirtonii* belongs to *Thesium* sect. *Imberbia* subsect. *Subglabra*.

*Additional materials studied.* – South Africa. WESTERN CAPE. **3420 (Bredasdorp)**: Luipaardskop 53, about 12 km NW of Wydgeleë, slopes between Suikerkankop, Kraaiheuwel and Rooikop Trig beacon 157 (-AD), elev. 220 m, 10 September 2000, *Helme 1744* (NBG!, STE!); on quartz-silcrete patches in Renosterveld, on the private farm, Spitskop, Overberg (-AD), elev. 245 m, 22 Match 2017, *Zhigila & Muasya 021* (BOL!, NBG!); upper parts of Sonderkoskop, along jeep track and slopes in the reserve Plaatjieskraal farm (-AA), elev. 302 m, *Zhigila & Muasya 022* (BOL!, NBG!, K!); along trial paths in Haarwegskloof Renosterveld Reserve, elev. 255 m, 22 March 2017, *Zhigila & Muasya 026* (BOL!, NBG!, K!); on SW flank of Milanskraal farm, elev. 195 m, *Zhigila 276* (BOL!, NBG!).


**Fig. 4.9:** *Thesium stirtonii*. A) Heath-like habit and quartz habitat (photo by J.P. Groenewald). B) Virgate branchlets with paniculate inflorescences C). Flowering and non-flowering shoots with scale-like leaves and attenuating tips in the latter. D) Much-branching habit. E and F) Flowering shoots. G) Fruiting- and attenuated shoots. H) Aerial view of a 6-merous flower showing the staminal filaments inserted at the junction between the perianth lobes and hypanthium. I**)** 7-merous flower. J) Longitudinal section of a flower showing the twisted placental column and subsessile stigma.

# CHAPTER FIVE

## 5.0 Habitat modelling, ecological correlates and extinction risk in the Greater Cape Floristic Region *Thesium* (Santalaceae)

### 5.1 INTRODUCTION

Ecological specialisation concerns how species restrict themselves to a range of environmental niches, with variation in niche breadth distinguishing ecological specialists from generalists (Clavel et al., 2010, Brennan, 2013). Specialists occupy narrow ecological ranges, while generalists occupy broad ranges, with a gradation between these two extremes (Kotze and O'Hara, 2003). In addition to occupying small geographic range sizes, specialists are mostly endemics and are restricted by how adaptable they are to environmental conditions such as climate or habitat breadth (Bott et al., 2013). In effect, specialists are usually less abundant, stationary and poor competitors (Cooper et al. 2008, Sodhi et al. 2008) and are sensitive to the slightest change (Hammond et al., 2018). Conversely, generalists are often wide-ranging, tolerate a variety of conditions (Devictor et al., 2010), respond less to external pressures (Hammond et al., 2018), and are more abundant because they are successful reproducers and competitors (Botts et al., 2013). Given the reported global warming (Urban, 2015), ecological specialists differ from generalists in that they are more vulnerable to decline, become threatened and ultimately suffer extinction (Clavel et al., 2011; Murray et al., 2011; Hammond et al., 2018). These factors suggest that well-documented environmental correlates that define species range sizes are vital in predicting future extinction rates (Bott et al., 2013).

The current comprehensive IUCN guideline would be improved if it allowed for a measure of ecological specialisation in its assessment criteria. South Africa adopted the internationally recognized IUCN guidelines for assessments of its national flora (redlist.sanbi.org, 2019). This adoption might proffer alternative measures to determining which species are more threatened under predicted environmental changes (Devictor et al., 2008; Morelli et al., 2019). Recently, data on the ecological preferences and habitat size ranges of species have been incorporated into IUCN Red List assessments (Breiner et al., 2017). Furthermore, since narrow-ranged species are mostly ecological endemics and occupy narrower niche breadth than wide-ranged species (Bott et al., 2013), additional information about the ecological specialisation of species might reveal the strength of persistence of species to environmental trajectories (Morelli et al., 2019). Regrettably, less than 5% of such information is provided for plant species, while in the equivalent data for animals about 75% of inscriptions on the IUCN database include their extinction risk assessments (Purvis et

al., 2000; Yessoufou et al., 2012; Yessoufou et al., 2016). In recent years, species distribution modelling (SDM) has been commonly used to predict species distribution ranges (Urbina-Cardona et al., 2019) and possible range shifts in response to climate change (Araújo et al., 2011; Rodríguez-Castañeda et al., 2012). Since extinction due to environmental change is historically-structured, models developed in the context of the present-day environment will highlight the past and future risk rate associated with climate change (Condamine et al., 2013). The analysis of species habitat suitability allows some understanding of how a taxonomic group is likely to respond to climate change scenarios (Turvey and Fritz, 2011; Yang et al., 2017; Lourenço-de-Moraes et al., 2019). In addition, it allows an assessment of which taxa have recovered and diversified following past extinction events (Chen and Benton, 2012; Condamine et al., 2013). Therefore, mapping species distributions on a fine scale grid using combined geological, topographical and climatic data facilitates insights into the nature of species range sizes (Kier and Barthlott, 2001; Elith et al., 2011; Keppel et al., 2017), helps predict patterns of local species diversity under current (Ferrier et al., 2002, Robertson et al., 2003; Guisan and Thuiller, 2005; Slatyer et al., 2007) and future climate change scenarios (Elith and Leathwick, 2009; Yang et al., 2017) and, by comparing the predicted species distribution and phylogenetic diversity patterns, assesses associated extinction threats (Pio et al., 2014).

The interplay between environmental correlates and the evolutionary history of a species is increasingly recognised as shaping the distributional range of species both temporally and spatially (Münkemüller et al., 2015). Interestingly, the signature of past evolutionary processes is commonly obtained from phylogenetic trees. These phylogenies can be used to account for the relatedness of species in biogeographic, comparative and evolutionary studies (Lavergne et al., 2010; Münkemüller et al., 2015). Intuitively, testing the phylogenetic signal of evolutionarily labile correlates such as ecological specialisation and extinction risks seems perversely illogical (Grandcolas et al., 2011). In plants, however, ecologically-predisposing conserved functional traits such as morphology, physiology, phenology (Willis et al., 2010) and evolutionary history are linked to species' response to their environment (ecological specialisation and vulnerabilities; Davies et al., 2011).

A comparative approach of testing extinction risks in the context of phylogenetic patterns vis-à-vis its impact on phylogenetic diversity can provide baseline information for conservation planning (Cardillo and Meijaard, 2012; Kelly et al., 2014). Presumably, lack of strong phylogenetic structure in extinction risks indicate that conserved functional traits and the ecological variables that determine species threats are independent of historical evolution. Conversely, strong phylogenetic signal suggests that extinction risks are shared among closely

related lineages (Yessoufou et al., 2016). Thus, if extinction risk is phylogenetically non-random, then interrogating the alternative evolutionary processes that best explain the distribution of threat status among tips of the phylogenetic tree might highlight functional traits significant to the extinction risk to species. Consequently, these might provide supporting information on forecasting imminent extinction risks (Kelly et al., 2014).

The Greater Cape Floristic Region (GCFR) is an ideal region for exploring the relationship of species vulnerability, because its physical environment (climate and geology) is complex and has facilitated the evolution of both strongly-stenotopic and more generalist species. Existing work suggests that within the GCFR, ecological specialists and narrow-ranged species tend to be concentrated in the western Cape Floristic Region (CFR; Cowling and Lombard, 2002) where moister conditions during the Pleistocene glacials (Chase and Meadows, 2007) may have provided a buffer against extinction (Cowling and Lombard, 2002; Cowling et al., 2015). This is in contrast to the drier conditions that prevailed in the east during glacials (Cowling and Lombard, 2002; Cowling et al., 2015). Similarly, greater climatic stability over time may account for the greater frequencies of ecological specialists observed in the western CFR (Cowling and Lombard 2002, Verboom et al., 2015). Notwithstanding their association with historically stable climatic refugia and narrow-range, ecologically-specialist species may be at particular risk of extinction, both because their associated cool conditions are expected to shrink disproportionately in the future (Ohlemueller et al., 2008) and because the small size of their ranges inherently increases their vulnerability to change (Hannah et al., 2005; Schwartz et al., 2006).

Having both range-restricted and widespread species, *Thesium* represents an appropriate system for assessing the correlates of range extent and specialisation and the relative extinction risks faced by narrowly-ranged versus widespread species due to accelerating climate change. This study therefore focuses on the GCFR *Thesium* clade (Moore et al., 2010), a largely Cape-endemic lineage that originated in the Middle Miocene and subsequently radiated to give rise to the bulk of *Thesium* species richness (ca. 100 species) found in the contemporary GCFR (SANBI, 2017; Chapter 2). The hypothesis that ecologically-specialist, narrow-range species are more vulnerable to climatic perturbation (Heuy et al., 2012) is tested. A second hypothesis being tested is whether specialism and climate change sensitivity are phylogenetically structured such that species losses are likely to produce a disproportionate loss of phylogenetic diversity (Eiserhardt et al., 2015). Finally, the specialism and range extent data are used to re-evaluate the conservation status of *Thesium* species. The approach followed involves: (i) generation of geospatial data in a Geographical Information System (GIS)

framework to quantify species range extent and ecological specialism, and assess whether these are correlated; (ii) development of distribution models for each species in the context of contemporary climates and assessing the impacts of projected climate change on the ranges of these species by using these models to predict distribution in 2080; (iii) assessment of the relationship between climate change response to ecological specialism and present-day range extent; and (iv) in the context of GeoCat (Geospatial Conservation Assessment Tool) framework (Bachman et al., 2011; IUCN, 2017), reassessment of the threat status for each species.

## 5.2 METHODS

### 5.2.1 Species data

A database for the distributions of all GCFR *Thesium* species was compiled using several sources including: i) the public-domain Botanical Database of Southern Africa (BODATSA) managed by the South African National Biodiversity Institute, Pretoria (www.sanbi.org), most of which are geo-referenced to the level of "quarter-degree square" (this refers to the national geographic grid of South Africa, coverage area ca. 25 × 25 km); ii) species occurrence records deposited at the Global Biodiversity Information Facility websites (GBIF, 2019); iii) records not currently captured in BODATSA or GBIF by South African and international herbaria having significant holdings of Cape plants *e.g.*, BOL, FHI, FHO, GRA, K, MO, NBG (SAM and STE inclusive), OFX, PH, PRE and S (codes following Thiers, (2019)); and iv) our own field records. The locality information was used to obtain coordinates by geo-referencing all specimens. At the geo-referencing stage, the coordinates of each specimen were given a precision code, making it possible to select specimen subsets based on locality precision. Doubtful records were projected against the ArcMap GIS 10.6.1 (2018) and unknown species point ranges were excluded accordingly.

Misidentification of *Thesium* species is a problem in many herbarium collections, because *Thesium* species are morphologically similar and notoriously hard to identify (Hill, 1925). To minimise misidentifications, all specimens were properly vetted against the type specimens. Species with less than four point-occurrence records were excluded from the model. Several studies, such as those by Hernandez et al. (2006) and Pearson et al. (2006), have demonstrated that small sample sizes distort the accuracy of SDMs (Wisz et al., 2008). Thus, only species with five or more occurrence data points were considered for further analyses. Also, species with multiple records (duplicates) from a single point or duplicate specimens from the same collector deposited at several databases were removed. Ultimately, of the 5 510

species records within the initial database, 3 576 specimens comprising 101 GCFR species were used for analyses (Appendix Table S5.1). Specimen distribution data were used to estimate the range extent (convex hull area and maximum pairwise distance between collections) and generate environmental variables associated with each species point, following Hijmans (2019).

### 5.2.2 Selection of environmental variables

The environmental niche of each species was characterised using geo-referenced present-day specimen localities and queried relevant environmental layers within a GIS framework using raster package version 2.9-5 (Hijmans, 2019) in R (R Core Team, 2019). Nineteen biologically-relevant climatic layers at 30" arc spatial resolution (fine scale with 1 × 1 km grid cells) were downloaded from Worldclim (2019). Temperature and precipitation records were summarised as means and standard deviations for: (i) the Last Glacial Maximum (LGM); (ii) the last 50 years until the year 2000, representing the present-day climate scenario (Hijmans et al., 2005); and (iii) the emission scenario projected by the Intergovernmental Panel on Climate Change (IPCC) of high representative concentration pathways (RCP 8.5) emissions for the year 2080 (Worldclim, 2019). Topographical and soil heterogeneity are drivers of species distribution at a regional and local scale, thus elevation layer (downloaded from http://www.worldclim.org) and eight soil variables (Cramer et al., 2019), totalling 28 *a priori* environmental data variables were included. Since strong multicollinearity among environmental correlates can cause model "overfitting" and compromises model precision (Boria et al., 2014, Feng et al., 2019), a multicollinearity test was performed using Pearson's correlation dimension-reduction methods (Pearson et al., 2006; Dormann et al., 2013) to minimise such effects and to determine the strongest environmental predictors of species range extents. An appropriate threshold of $r > 0.7$ (Dormann et al., 2013) of the species presence points in the variables were considered highly correlated and thus only one of such variables was systematically retained for the model (Appendix Fig. S5.1). Ultimately, 14 noncollinear variables including seven soil variables, six climatic variables and elevation (Appendix Fig. S5.1) were used for the ecological niche modelling. Presumably, elevation and soil data will remain relatively constant up to the year 2080 and therefore these contemporary data were used to perform the habitat suitability tests over time (Lourenço-de-Moraes et al., 2019).

### 5.2.3 Quantifying species range extent and ecological specialization

To quantify the range sizes of species and to test whether they were correlated with species ecological specialization, minimum convex hull polygons and maximum distance relating to

the species-specific standard deviation of each environmental variable were used. According to Burgman and Fox (2003), where point occurrence data are available, generating a convex hull polygon for a set of points is an accepted method for estimating the range size of a species. The strength of this method is its simplicity, but it has been criticized for bias in overestimation of habitats of species, given variations in habitat shapes and underlying sampling lapses, both temporally and spatially (Burgman and Fox, 2003; Preuss et al., 2014; IUCN, 2017). In this study, these errors were relatively controlled by employing an additional maximum distance method (α-hull), which provides explicit ways of expunging unoccupied gaps (*e.g.* rivers) in a species range (Burgman and Fox 2003; IUCN, 2017).

The ecological specialism of a species was estimated by determining the standard deviation for each environmental variable across its occurrence localities. Following Júnior and Nobrega (2018), these variables were then summarised using a principal component analysis (PCA) to derive an overall index of specialism. The specialism index was derived as the first axis) of a PCA based on the standard deviations of the environmental variables, which were first z-standardized to normalise the data. This was performed within the built-in R function prcomp (R Core team, 2019). Then, variation in specialism and range extents were summarized using histograms and scatterplots with the package ggplot2 version 3.2.0 (Wickham, 2016). The ordination derived was used to test the prediction that ecological specialists would have a lower standard deviation relative to the mean, while generalists would be expected to have wider values.

### 5.2.4 Species distribution modelling

To test the hypothesis that narrow-range/ecological specialist species are more prone to extinction than generalists under predicted climate change scenarios, we modelled the conditions for the Last Glacial Maximum (LGM), for the present-day, and for the future of all GCFR clade species using MaxEnt (Phillips et al., 2006; Elith et al., 2011) as implemented in the dismo package (Hijmans et al., 2017; 2019). The MaxEnt model is the most used package for SDMs (Phillips et al., 2017; Soberon et al., 2017; Urbina-Cardona et al., 2019) and was developed in the context of chosen contemporary environmental layers. For generating the model, 75% of the occurance data of each species was used to train the algorithm and the remaining 25% used as test data. The model quality was evaluated using the area under the receiver operating characteristic curve (AUC) values. An AUC score of < 0.8 was considered random, from 0.8 to 0.9 was good, and > 0.9 was excellent (Fielding and Bell, 1997). The use of AUC values as a measure of model performance has been criticized due to computational

limitations in case of modelling species with few data points (Van Proosdij et al., 2016). As stated above, species with few records (< 4 data points) were removed. In addition, null model test was employed for improved performance and for reliable species distribution models (Van Proosdij et al., 2016). Thereafter, using the models thus derived, retrospective species distributions using the environmental layers from the last glacial maximum (LGM, to about 22 000 years ago) were predicted. To test the hypothesis that ecological specialists are at greater risk of extinction due to rapidly increasing climate change (Peterson et al., 2012; Morueta-Holme et al., 2013; Sandel et al., 2017), a similar approach as above was employed, except that species ranges forward in time were predicted using environmental layers for the year 2080. By comparing the projected ranges of species at that time with their contemporary ranges, it was possible to quantify, for each species, the absolute area of climatically-suitable habitats that will remain in 2080, the percentage of range loss or expansion, the measure between the contemporary and projected ranges, and the extent to which species ranges differed.

### 5.2.5 Phylogenetic tree estimation

The matrix of aligned DNA sequences of *Thesium* (Zhigila et al., 2020; Chapter two) was used to reconstruct a phylogenetic tree. The DNA sequences consist of a concatenated nuclear (ITS) and three plastid gene regions (*matK, trnL-F* and *rpl32-trnL*). The phylogenetic tree obtained from these sequences represents the most updated current genus tree for *Thesium* (Zhigila et al., 2020). A Maximum Clade Credibility (MCC) tree was generated in BEAST2 version 2.5.2 (Bouckaert et al., 2019). For the molecular evolution model, GTR + I + Γ was chosen (Yang et al., 2017) for both partitions using ModelTest-NG (Darriba et al., 2019). For time calibration and construction of BEAST-derived chronograms, Moore et al. (2010) was followed. The resulting chronogram was imported into R to trim outgroups, the non-GCFR species and duplicate accessions to match the spatial data matrix species.

### 5.2.6 Testing phylogenetic signal

To assess relative to the phylogenetic hypothesis, whether range size, ecological specialization and extinction risk are phylogenetically structured (*e.g.* species at greatest risk or generalists vs specialists are closely related) and, therefore, the extent to which future climate change might influence the overall phylogenetic diversity of the *Thesium* GCFR clade, Blomberg's *K* (Blomberg and Garland, 2002) and Pagel's λ (Pagel, 1999) models were used. The statistical model for continuous trait values among species is measured via phylogenetic signal (Blomberg and Garland, 2002; Harmon et al., 2019). Thus, phylogenetic signal has the power

to show species with higher extinction risk as being clustered on the phylogeny (Thuiller et al., 2011). It was expected that the null would be a random pattern in the data, thus only *K* or λ-values with significant *p*-values (> 0.05) were interpreted as structured patterns, i.e. having a strong phylogenetic signal. For both *K* and λ, a total of 999 randomisations were used to compute the *p*-values. The phylosignal functions of the *picante* and *geiger* packages (Kembel et al., 2010; Keck, 2019) and (Harmon et al., 2019) were respectively used in R to calculate these statistics.

### 5.2.7 Species risk assessments

Substantive assessment of species conservation status is based on a comprehensive consideration of the five criteria (A–E) outlined in the international IUCN Red List Criteria guidelines (IUCN, 2017). Nevertheless, the appropriate assessment is establishable if at least one criterion is met (IUCN, 2017; Moat et al., 2018; Lourenço-de-Morae et al., 2019). As the detailed population-level and quantitative data of the GCFR *Thesium* species are limited, the geographical ranges of species were used to assess their extinction risk. Theoretically, this measure is the key requirement of the IUCN 'B' criterion. For this, the package GeoCAT (Geospatial Conservation Assessment Tool, Bachman et al. (2011); Moat et al. (2018)) was downloaded from http://geocat.kew.org/ and was used to measure the extent of occurrence (EOO, "measure of the geographic range size of a species") and the area of occupancy (AOO, Willis et al., 2003) of each species. The default 2 × 2 km cell size recommended by IUCN (2017) and Moat et al. (2018) was kept for the analyses. Accordingly, based on the geographic range sizes, the following risk categories, in context of a local-scale occurrence, were proposed: i). Extinct (EX) = 0 $km^2$; ii). Critically Endangered (CR) = < 100 $km^2$; iii). Endangered (EN) = < 5,000 $km^2$; iv). Vulnerable (VU) = < 20,000 $km^2$; v). Near threatened (NT) = < 40,000 $km^2$ and vi). Least Concern (LC) = > 40,000 $km^2$ (IUCN 2017; Lourenço-de-Morae et al., 2019).

## 5.3 RESULTS

### 5.3.1 Quantification of niche breadth

The frequency distribution quantifying habitat niche and range extent of the GCFR *Thesium* species is illustrated in Fig. 5.1. Precipitation of the wettest quarter representing rainfall variables displayed a bell-shaped spread (Fig. 5.1A), indicating reduced range size as precipitation increases above a certain threshold value. A similar curve was true for temperature (represented by isothermality, Fig. 5.1B) and soil (represented by pH, Fig. 5.1C). In terms of elevational niche, the range was normally distributed across taxa, with most species having a standard deviation of < 400 m (Fig. 5.1D). Most species lay between being strongly-specialist (< 100 m) and highly indiscriminate (> 800 m). The temperature and rainfall variables corresponded with the elevation range in the GCFR mountainous areas at which there was a relatively high rainfall and reduced temperature. The range size values indicated that the standard deviations of the geographic distribution coverage of the GCFR *Thesium* vary from 2.5 to 1200 $km^2$ with ca. 80 species having ranges < 700 $km^2$ (Fig. 5.1E). The curve became stable indicating an increase in range size for about 20 species. The distance of the standard deviation from the overall mean of each variable as the function of the degree of specialisation for a species was estimated. The derived specialisation index showed a skewed left distribution with few species showing strong specialism (Fig. 5.1F).

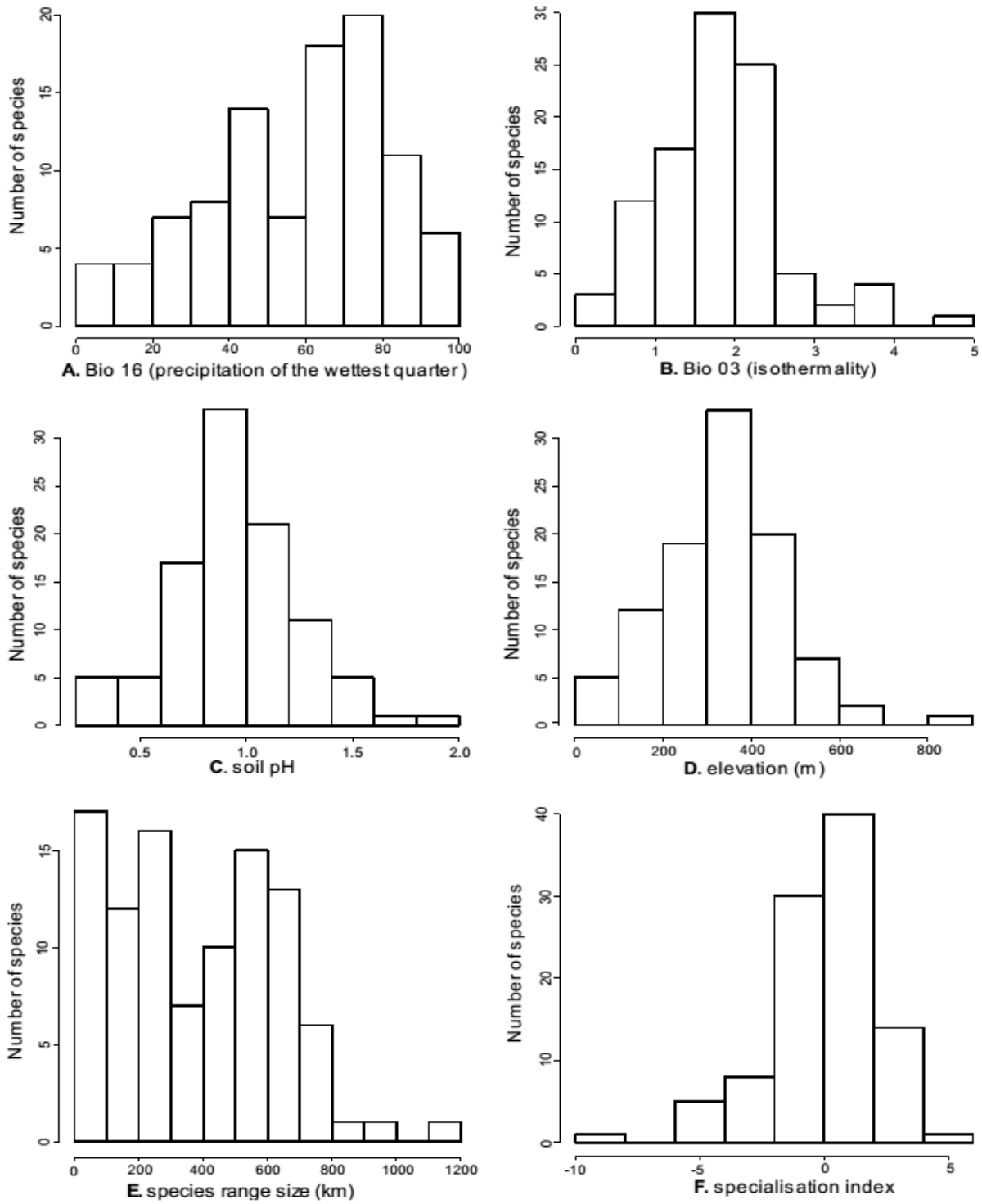



**Fig. 5.1:** Histograms illustrating the cross-species distributions of standard deviations of A) Bio16 precipitation of the wettest quarter, (as an example of rainfall), B) Bio 03 isothermality (as an example of temperature variable), C) soil pH (as an example of an edaphic variable), D) elevation, E) species geographic range size ($km^2$), and F) values for the first principal component as an index of specialisation.

The PCA applied to species-specific standard deviations of the 14 environmental variables (Appendix Table S5.2) and summarised the total ordination dimensionality, PC1 (31.6%) and PC2 (16.2%) as the dominant axes (Fig. 5.2). Negative scores correspond to small standard deviations of environmental variables, positive scores with larger standard deviations. All variables correlated positively with the first principal component (hereafter referred to as specialism index), identifying this axis as a major index of specialism (niche breadth). The axis identifies species on the left of the plot as specialists and those on the right as generalists. Where the soil related variables generally contribute positively (positive loadings) to PC2, elevation and bioclimatic variables (except mean diurnal range and isothermality) contribute negatively to PC2 (Fig. 5.2; Appendix Table S5.3). Hence, PC2 describes the relative importance of soil as opposed to climatic variables underpinning specialisation. Thus, of the 101 species (Appendix Table S5.3), the separate quantification of ecological specialisation classified 61 species as specialists (of which 34% are habitat specialists and 66% are climate specialists) and 40 species as generalists (48% habitat generalists and 52% climate generalists). Based on the predefined specialisation threshold, ten species (9% of the GCFR *Thesium* species) could not be classified with confidence due to their rarity and limited occurrence records ($\leq 4$ occurrence points). For details of PCA loadings and scores, descriptions of environmental correlates, standardized data matrix and species names, see Appendix Table S5.3, Table 5.4 and Appendix Table S5.2, respectively.

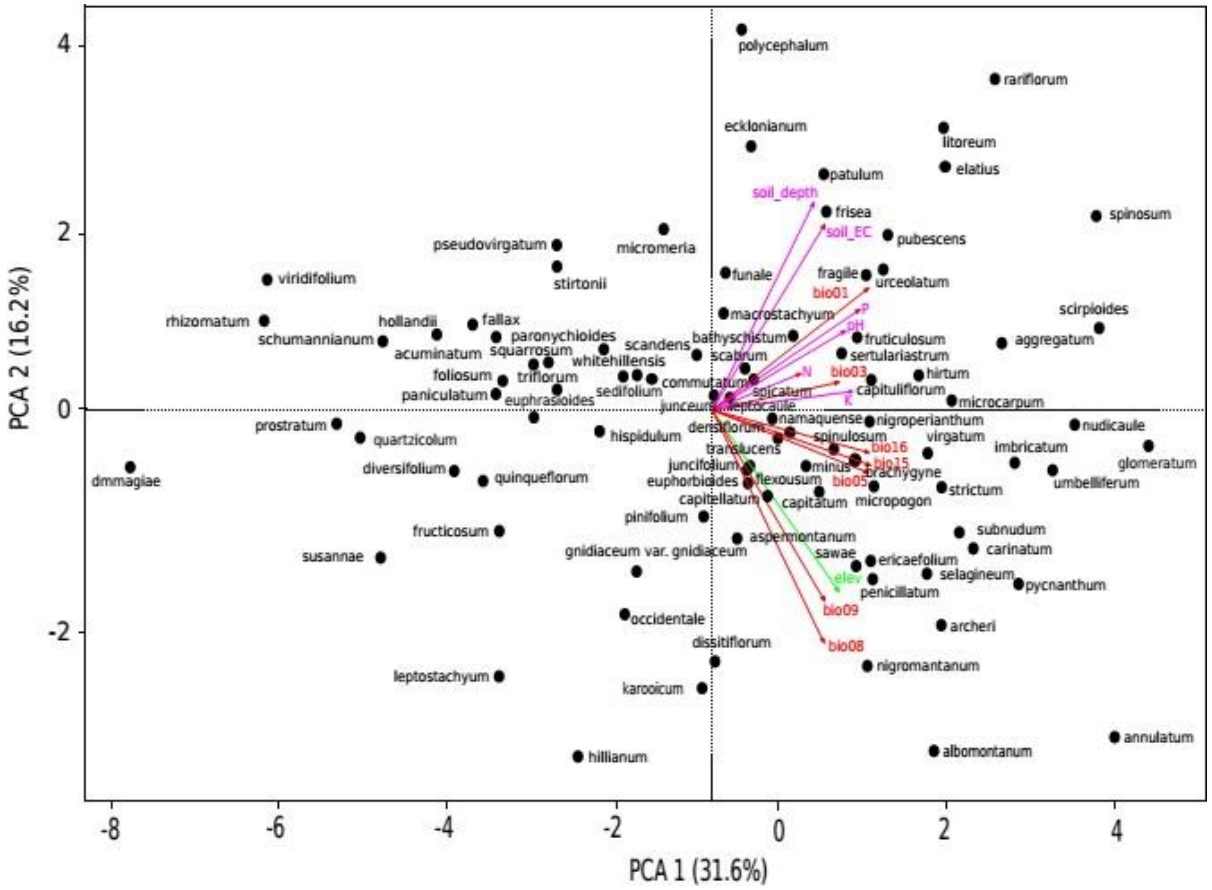



**Fig. 5.2:** Principal Component Analysis (PCA) plot applied to the GCFR *Thesium* species-specific deviations from the original means of environmental correlates. The ordination scores for each species are represented by black dots. *Post hoc* variable vectors as determined by the PCA axis loadings with bioclimatic, elevation and soil data are indicated in red, green and magenta, respectively.

### 5.3.2 Correlation between range extent and ecological specialization

There was a strong positive linear relationship between each environmental variable and species mean range size (Fig. 5.3). However, three variables (maximum temperature of warmest month, soil K and soil total N) showed no correlation (Fig. 5.3C, K and L). On average, widespread species showed greater ecological breadth and narrow-range species stronger ecological specialism. The strong positive correlations observed were supported by the significant *p*-values of the square of the correlation coefficient ($r^2$) in most variables. These indicate positive correlations in climate specialists rather than habitat specialists relative to their respective generalists. Similarly, the plot of species ecological specialisation (PC1) and the distribution range sizes (m) showed a strong positive linear correlation (Fig. 5.3). This relationship is supported by a significant regression coefficient value of species dispersion ($r^2 = 0.36$, $p < 0.0001$).

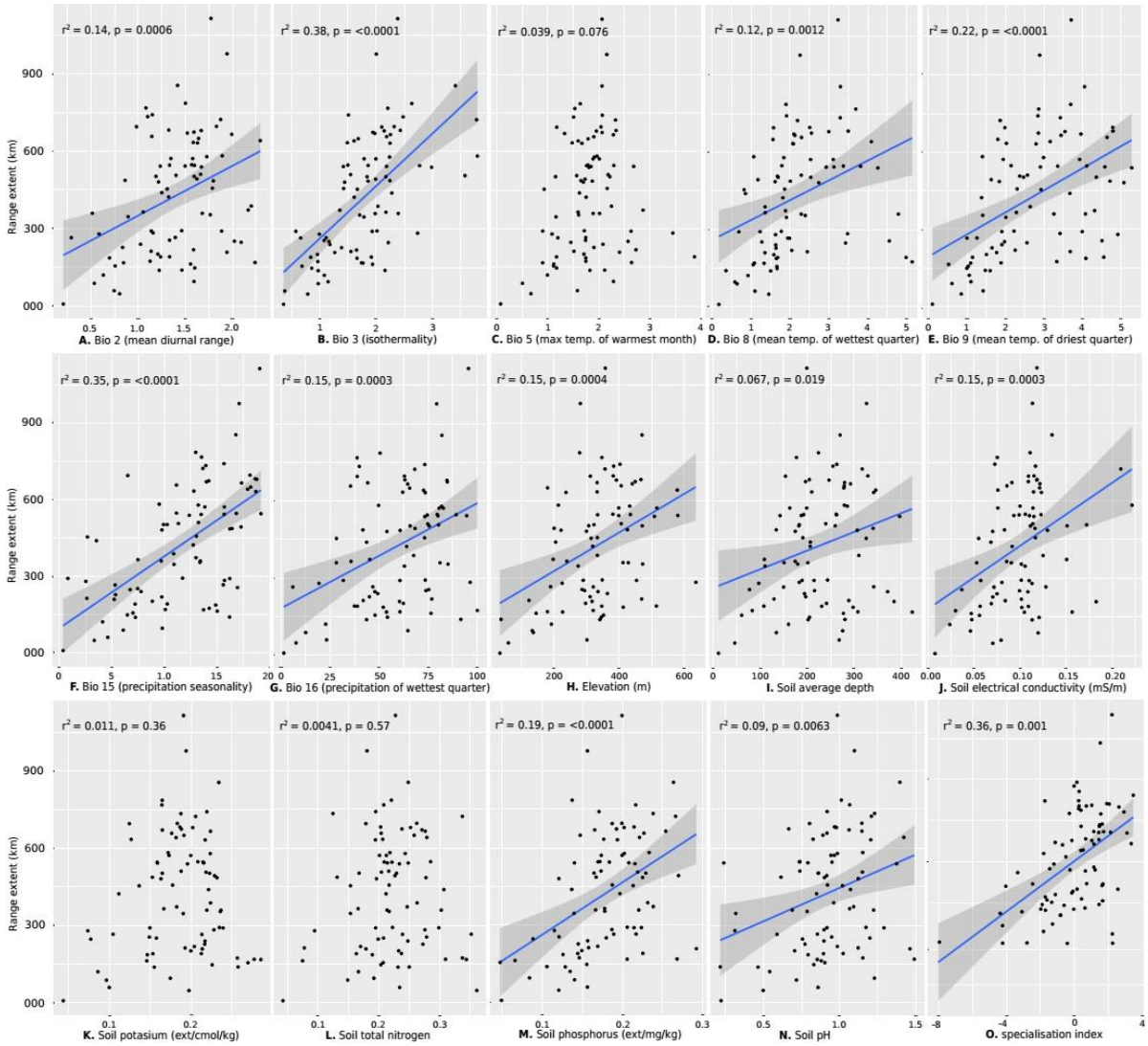



**Fig. 5.3:** Assessment of correlation between the average range extent of individual species (maximum distance (m)) and the standard deviation of each environmental variable. Values obtained from PC1 were used as the index for specialisation to evaluate the relationship between species range extent (m) and ecological specialisation. Figures were plotted on logarithmic models and fitted on logged means of species values. Lines indicate best linear fit for each species and the grey bands are the 95% confidence levels. The square of correlation coefficient ($r^2$) and the corresponding p-values are included at the top left corner of each panel.

### 5.3.3 Species distribution and predictions

The 101 *Thesium* species modelled exhibited a diverse array of range size changes in response to the three climate scenarios explored (Fig. 5.4; Appendix Table S5.6). Of these, 71 species (83%) are inferred to have had larger ranges during the LGM than at present. The remaining 30 (17%) showed an increase in range size from the LGM to present. Forty-five species (44%) are predicted to expand their ranges between now and 2080, while 51 (50%) are predicted to experience range contraction. Interestingly, five species (5%), although

experiencing range reduction from the LGM to present, are predicted to maintain their range sizes and persist in the face of future climate change. Importantly, no species are expected to lose their range entirely. There was no correlation between predicted range size change and present-day range size or ecological specialism (Fig. 5.4A, B). The frequency of range size contractions was remarkable in some species (Appendix Table S5.6), for example *T. selagineum* and *T. fallax* showed the highest contraction with (89%) each, followed by *T. stirtonii* (55%). Interesting, there was an increase in the predicted range size of some species, with *T. hollandii* predicted to experience the highest increase (69.6%), followed by *T. archeri* (54.3%) and *T. quartzicolum* (54.1%). In species, such as *T. bathyschistum*, the increase in range size indicates resilience to environmental change. There is a negative relationship between the nature of range change between the LGM and the present, and of that between the present and 2080. This implies a tendency for species whose ranges have contracted since the LGM to expand in the future, and *vice versa* (Fig. 4.5C and D, Appendix Table S5.6). For details of the predicted range change over time of each species, see Appendix Table S5.6.

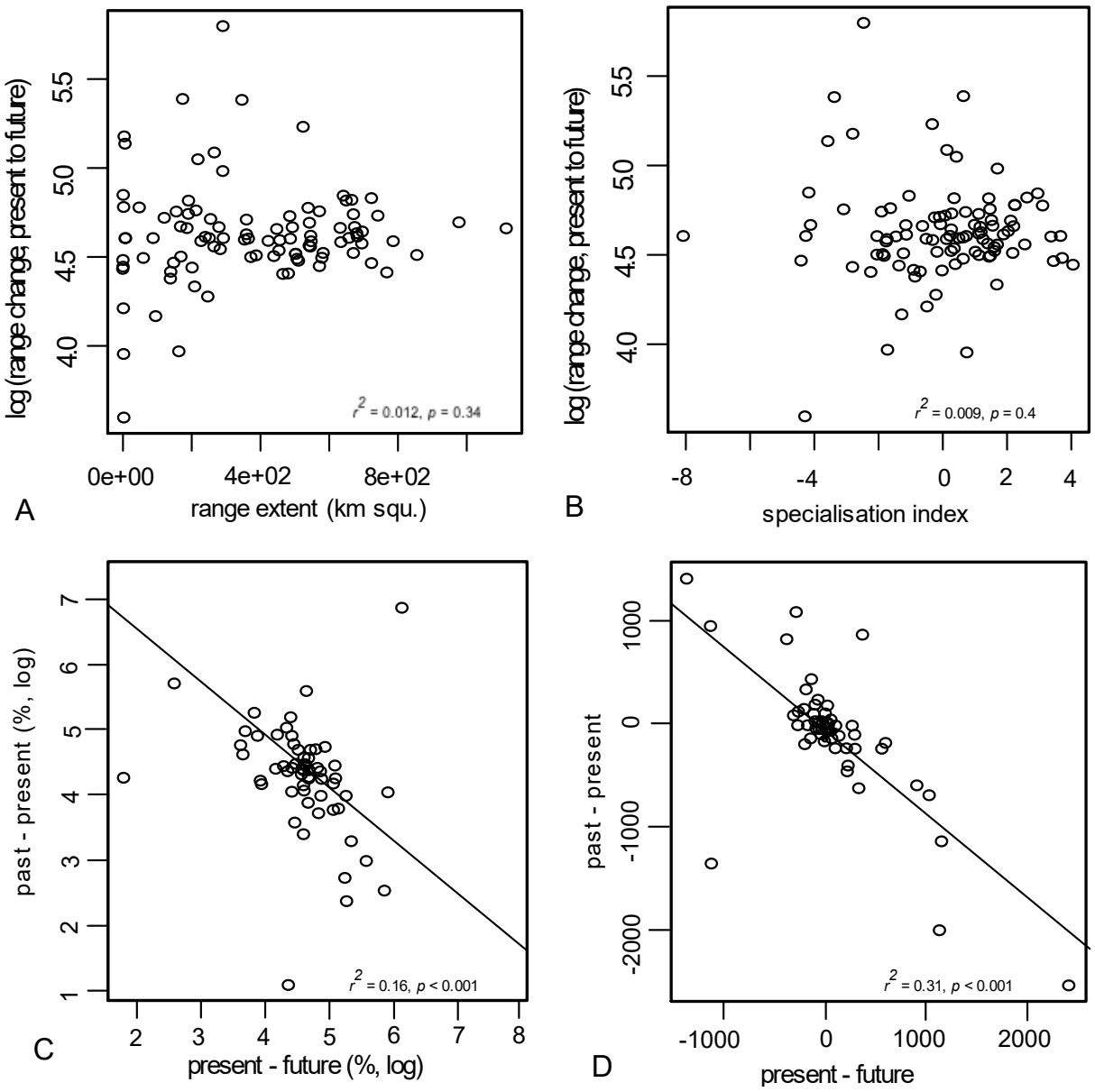



**Fig. 5.4:** Correlation between A) log-transformed changes in range extent ($km^2$) and present to future range change (%), B) specialism index (PC1) and range change from the present to future (%). Predicted range expansion or contraction difference from C) the past to future in relation to the present to future (2080) expressed in log-transformed percentages and D) absolute range change values from the past to present and the present to future. Each dot represents a species. The square of the correlation coefficient ($r^2$) and the corresponding p-values are included at the bottom right corner of the panel.

For most species, distribution models identified climatic variables as better predictors of suitable habitat than soil and elevation variables. Although the predictors can be viewed as continua, 84 species had primarily climatically-driven distributions with climatic variables

having 45–91% estimated contribution; *e.g.* for *T. capitellatum* Bio 2 (mean diurnal range) and Bio 16 (precipitation of wettest quarter) were the main correlates of habitat suitability for this species (Appendix Table S5.6). Eighteen species had primarily edaphically-driven distributions with strong edaphic influence observed in *T. gnidiaceum* (mostly pH and N), with 36%–40% variable contributions. However, the remaining soil variables contributed to only one species each (Appendix Table S5.5). The distribution of 15 species (with 42%–60% relative contributions) were predominantly driven by elevation. Of the 15, 11 species distributions were mostly influenced by low elevation (mean elevation < 200 m a.s.l), *e.g. T. rufescens*, and four species had high elevation as the main distribution driver (mean elevation > 1000 m a.s.l), *e.g. T. annulatum.*

The AUC values for the predicted species distribution over time were high, with an average of 0.925 (0.801–0.998, Appendix Table S5.6; Fig. S5.2). Such high values demonstrate a reasonable predictive performance of the model. In addition, the omission rate increased linearly with occurrence probability (Appendix Fig. S5.2). Also, the relatively low values between omission rate and the predictive probability of occurrence support the preference and suitability of the model. Generally, the three climate change scenarios yielded similar predicted distribution ranges for species of *Thesium*. Hence, we present predictions for exemplar species only (Fig. 5.5). The predicted habitats of the GCFR *Thesium* species with climatically-determined ranges attained their maximum range extents in the LGM (ca. 22,000 years ago), *e.g. T. fallax*, as opposed to edaphic-specialists and generalists, *e.g. T. bathystichyum* (Fig. 5.5a–f). In contrast, the present and future scenarios predicted range expansions in generalists, *e.g. T. selagineum* (see Fig. 5.5b, bar plots at the right corner of each exemplar species). Overall, coastal areas of the northwest, southwest and toward the southeast are predicted as having the highest habitat suitability for most *Thesium* species relative to the arid fringes of the GCFR (Fig. 5.5). For example, the projected suitable habitats for *T. minus* over the three periods span its actual geographical range (Fig. 5.5c). The predictions indicate that this species' suitable habitat spanned from the northwest coasts to the nouthwest coasts of the Cape Peninsula with a disjunct distribution into fringes of the Karoo Mountains and towards the southeast coasts during the LGM. Although there was increase in range size from the LGM to the present, 61% of its present range is predicted to be greatly reduced in future (Fig. 5.5c). The probable contraction in range size for this species is mainly influenced by climatic variables (bio02, bio16 and bio05) and elevation in descending order of variable contributions.

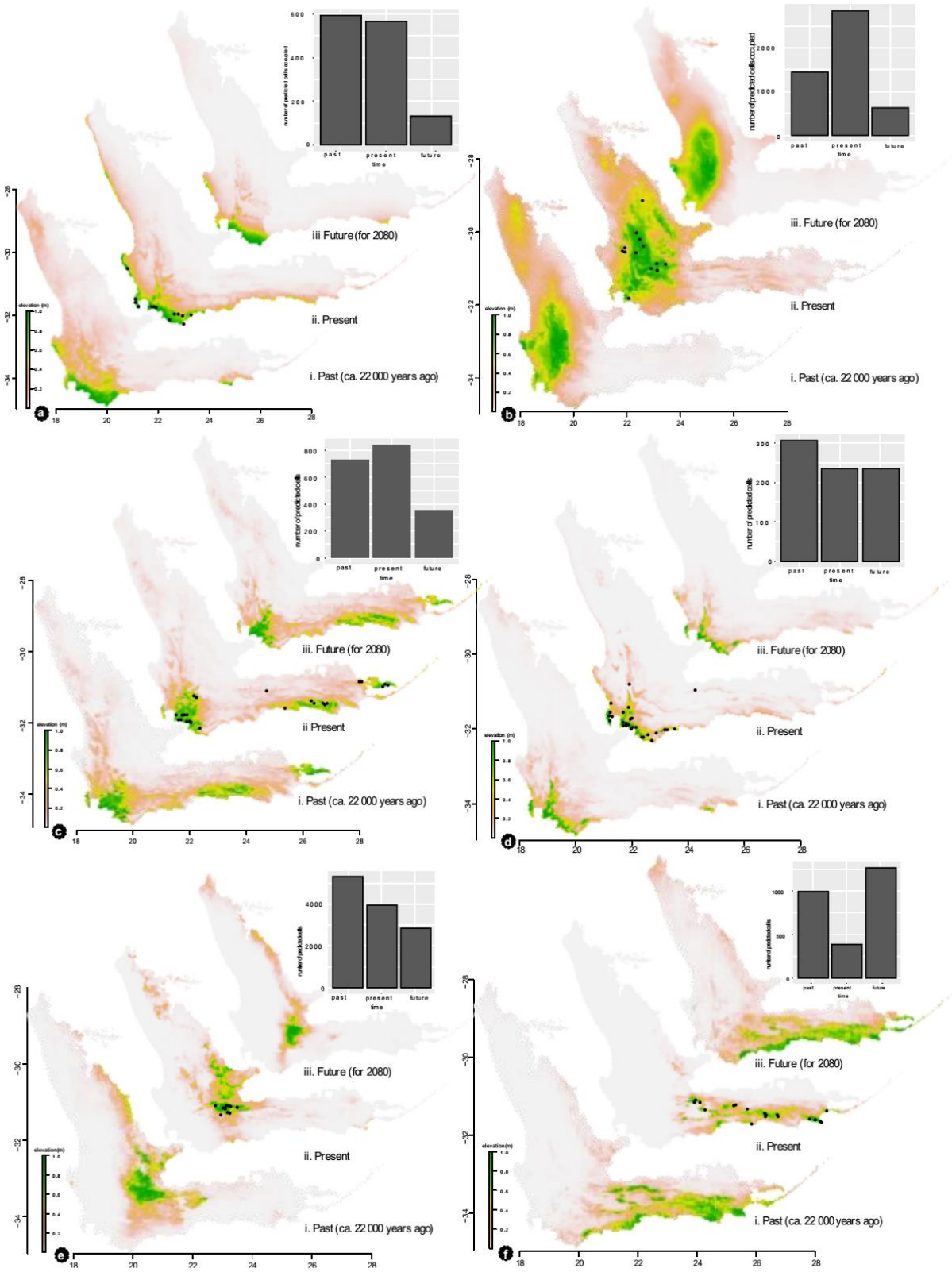



**Fig. 5.5:** Predicted distribution ranges for exemplar species (i) backward projections to the Last Glacial Maxima (LGM), (ii) under contemporary conditions and (iii) in the future. The predictions were based on species-specific MaxEnt models. The green colour indicates areas with highest suitability probability grading to lowest greyish white areas. Filled circles plotted on the present-day model prediction are the actual species occurrence localities. Bar plots at

top right corner compare variations in the cell frequency (range extent) of the species over time. The threshold probability of occurrence being < 0.5 equals 0 (absent), while > 0.5 to 1 equals 1 (present). The bars indicate estimated percentage range loss of each species from the LGM, contemporary suitable habitats to future, year 2080. (a) *Thesium fallax*, (b) *T. selagineum*, (c) *T. minus*, (d) *T. bathyschistum*, (e) *T. whitehillensis*, (f) *T. hollandii*.

### 5.3.4 Phylogenetic signal

There was a similar pattern for Blomberg's *K* and Pagel's λ in phylogenetic signal values obtained (Table 5.1). Specialisation in all environmental variables, species range extent (maximum distance) and extinction risk values showed low phylogenetic signal based on Blomberg's *K* and Pagel's λ (at $p < 0.05$). The observed variance in phylogenetic independent contrasts (PICs) and their corresponding means of the environmental variables support the *K*-value, except for soil traits (with exception of soil average depth) and mean diurnal range (Table 5.1). This means that any phylogenetic patterns observed in the GCFR *Thesium* clade is a function of random variation rather than selection or convergent evolution. In other words, the predictiveness of phylogenetic signal tests are labile with respect to detecting any pattern in the clades.

**Table 5.1:** Phylogenetic signal for the variance of each environmental trait inferred from the phylogenetic tree of the GCFR *Thesium* species. The outputs are (a) Blomberg's *K* and (b) Pagel's λ-values and the associated p and tip-permutation test values. *P*-values are reported at < 0.05 level of confidence. Standard deviation of each variable was log-transformed. Phylogenetic independent contrast (PIC), Bio2 (annual mean temperature), Bio 3 (isothermality), Bio 5 (maximum temperature of warmest month), Bio 8 (mean temperature of wettest quarter), Bio 9 (mean temperature of driest quarter), Bio 15 (precipitation seasonality), Bio 16 (precipitation of wettest quarter), K (Potasium), N (Nitrogen), PC (principal component).

| | (a) Blomberg's *K* | | | | (b) Pagel's lambda (λ) | |
|---|---|---|---|---|---|---|
| | *K*-values | PIC.variance.obs | PIC.variance.rnd.mean | *p* (rep = 999) | λ-values | *p* (rep = 999) |
| Soil depth | 0.2274 | 2858.24 | 3336.4475 | 0.132 | 0.0001 | 1 |
| Soil EC (mS/m) | 0.1861 | 0.0006 | 0.0006 | 0.573 | 0.0001 | 1 |
| Elevation (m) | 0.1636 | 9793.50 | 8492.0411 | 0.873 | 0.1038 | 0.304 |
| Soil K (ext/cmol/kg) | 0.1581 | 0.0034 | 0.0028 | 0.828 | 0.0022 | 1 |
| Soil N | 0.1633 | 0.0019 | 0.0016 | 0.93 | 0.0001 | 1 |
| Soil P (ext/mg/kg) | 0.1913 | 0.0014 | 0.0014 | 0.509 | 0.0101 | 1 |
| Soil pH | 0.1866 | 0.0366 | 0.0362 | 0.561 | 0.0001 | 1 |
| Bio 01 | 0.1777 | 0.1027 | 0.0978 | 0.668 | 0.0007 | 1 |
| Bio 03 | 0.1833 | 0.2666 | 0.2587 | 0.61 | 0.0001 | 1 |
| Bio 05 | 0.1431 | 0.3198 | 0.2431 | 0.978 | 0.1358 | 0.216 |
| Bio 08 | 0.2041 | 0.4574 | 0.4966 | 0.269 | 0.0001 | 1 |
| Bio 09 | 0.2029 | 0.718 | 0.7769 | 0.29 | 0.0231 | 1 |
| Bio 15 | 0.164 | 13.5844 | 11.819 | 0.86 | 0.0001 | 1 |
| Bio 16 | 0.1644 | 260.91 | 227.6382 | 0.871 | 0.5017 | 1 |
| Convex hull area (m) | 0.1696 | 1.28E+21 | 1.15E+21 | 0.751 | 0.0616 | 1 |
| Maximum distance (m) | 0.1411 | 3.69E+10 | 2.7646E+10 | 0.995 | 0.0092 | 1 |
| PC 1 | 0.1764 | 2.0683 | 1.9387 | 0.704 | 0.0012 | 1 |
| PC 2 | 0.1861 | 0.8747 | 0.8634 | 0.551 | 0.0001 | 1 |
| past-present | 0.2118 | 95645.62 | 100027.66 | 0.419 | 0.0064 | 1 |
| present-future | 0.1862 | 77678.92 | 76301.61 | 0.528 | 0.0083 | 1 |

Mapping species range extents, ecological specialisation and extinction risk on the MCC tree revealed a lack of phylogenetic structure, consistent with the Blomberg's *K* and Pagel's λ tests. The model does not identify specialist versus generalist clades on the phylogenetic tree (Fig. 5.6A–D). Thus, these factors are more random among close lineages compared with distant relatives in the GCFR *Thesium* clades. These findings indicate that range size and specialism are evolutionarily labile in *Thesium*.

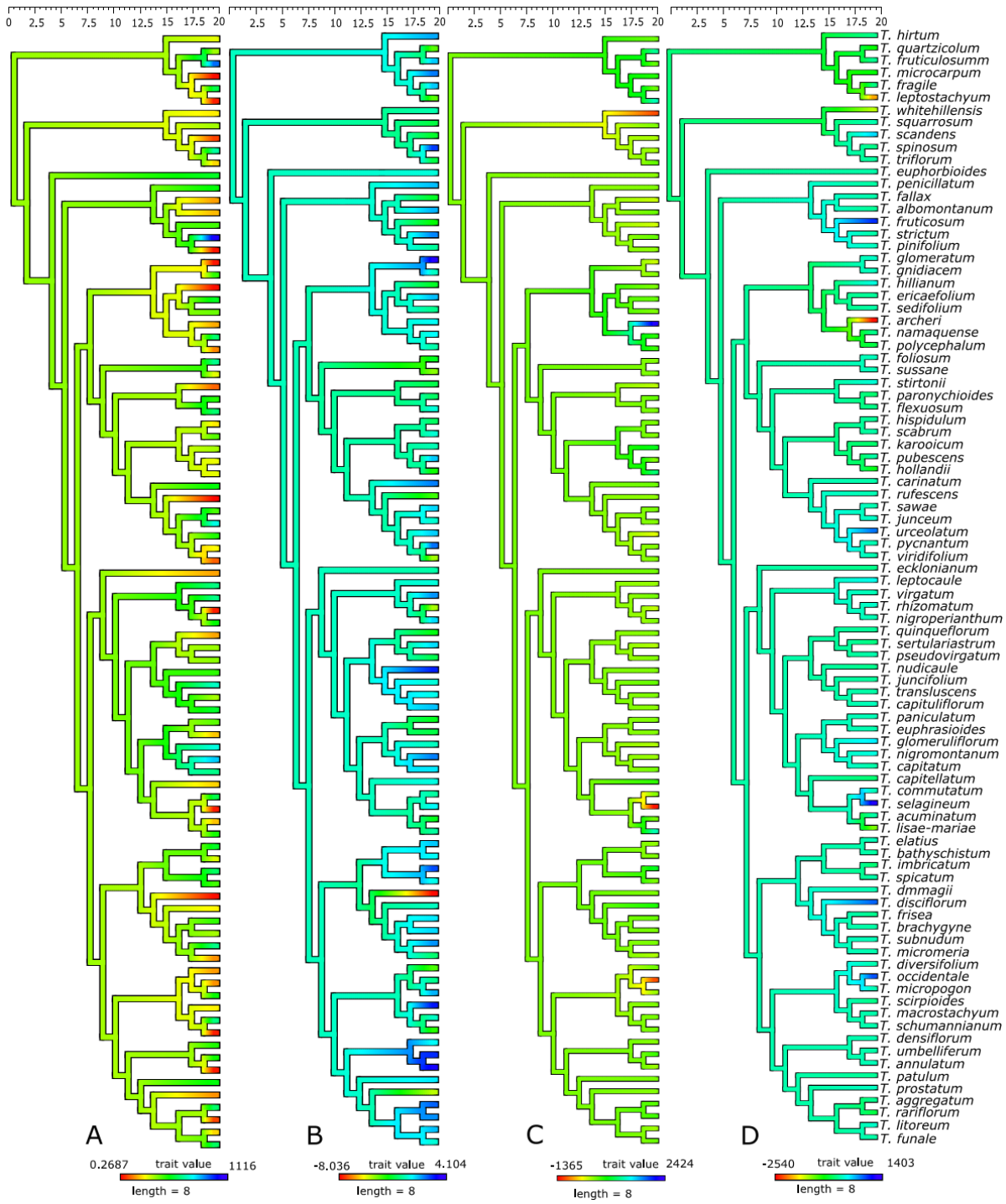



**Fig. 5.6:** Phylogenetic signal mapped on a Maximum Clade Credibility (MCC) phylogenetic tree. (A) range extent (maximum distance (km)); (B) first principal component values as specialisation index; and (C) estimate of cell frequency of species range change from past (LGM) to present (contemporary to 2080); (D) estimate of cell frequency of species range change from present to the future (year 2080). The phylogenetic tree was obtained from a concatenated nuclear (ITS) and three plastids (trnL-F+matK+rpL32-trnF) markers. Phylogenetic signals for ecological specialists (in red) grading to generalists (in blue) are indicated by clades and tip colours (note the colour ramp for interpretation of patterns).

### 5.3.5 Threat assessments

The assessment for threat level among species indicates an increase in the number of species with conservation concerns (Fig. 5.7; Appendix Table S5.7). Of the 101 GCFR *Thesium* species assessed here, four are Critically Endangered with EOO < 100 km$^2$; 18 are Endangered with EOO < 5,000 km$^2$; 22 are Vulnerable with EOO < 20,000 km$^2$; 17 are Near-Threatened with EOO of < 40 0000 km$^2$; and 41 are Least Concern with EOO > 40 000 km$^2$. Here, it is important to clarifythat this assessment was not intended to provide the conservation status of the GCFR *Thesium* species, but rather baseline information on the extinction risk imposed by accelerating climate change. See Appendix Table S5.7 for comparative threat status of each GCFR *Thesium* species.

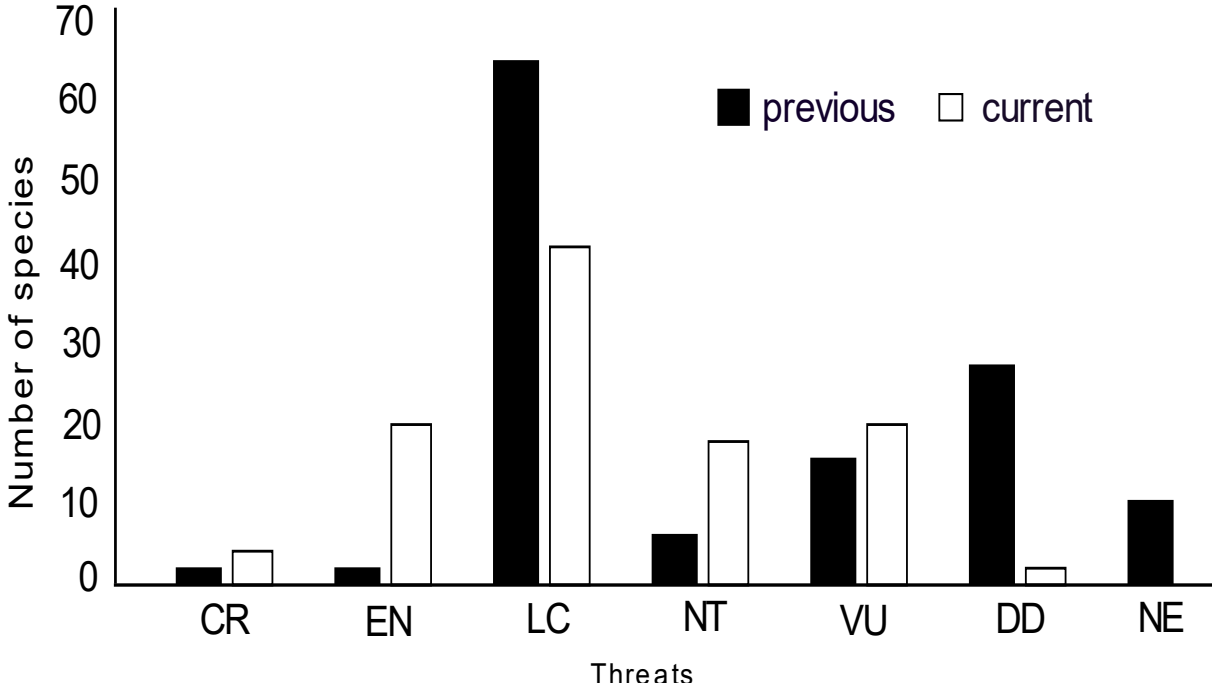



**Fig. 5.7:** Comparative Threat assessments of the GCFR *Thesium*. Previous assessment (solid bars) was obtained from redlist.sanbi.org (2019). The extent of occurrence (EOO) and the actual area of occupancy (AOO) were used to estimate and update the red list status of each species. Based on the species' distribution range (km$^2$), update on the threat categories at a local context for the GCFR *Thesium* is here proposed: Critically Endangered (CR), Endangered (EN), Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Data Deficient (DD) and Not Evaluated (NE).

## 5.4 DISCUSSION

Range extent and ecological specialism of GCFR *Thesium* species were estimated (Fig. 5.1). The standard deviation of species range extent was normally distributed, with most GCFR *Thesium* species having a narrow range deviation of less than 400 $km^2$. Only a few species are wide-ranging, with ranges up to 900 $km^2$ (Fig. 5.1). Species with a range extent of less than 400 $km^2$ were also specialists and predictably confined to areas of high endemism, *e.g. T. dmmagiae.* Meanwhile, an increase in species range size indicates generalisation and such species occupy areas of wide variability (Barret, 2013). Such range size distributions have been observed in several plant and animal taxa globally (Davies et al., 2011). Consistent with the specialisation-disturbance theory, which is largely supported in ecology, conservation and evolution literature (*e.g.*, Vazquez and Simberloff, 2002), the model derived a strong positive linear correlation between the species-specific environmental niches as a function of their range extents and the species overall ecological specialisation (Fig. 5.3). However, Vamosi et al. (2014) suggested that a species might be a generalist under one perspective, but a specialist under another, depending on the influence of the evolutionary and environmental trade-offs of a species (Davies et al., 2011). Yessoufou et al. (2016) reported that species range sizes correlate with their suitable environmental conditions. Therefore, it follows that environmental heterogeneity becomes a key trait in the evolution of ecological specialisation (Vamosi et al., 2014).

The distribution ranges for each GCFR *Thesium* species were modelled under contemporary conditions and then used to predict distributions for the LGM and for the year 2080. Despite there being a slight variation across species in the genus, the main determinants of *Thesium* range size are mean diurnal range, max temperature of warmest month, precipitation of wettest quarter, elevation, soil pH and soil nitrogen (Fig. 5.1). Consistent with previous studies, these variables are considered the most important biological drivers of habitat suitability across GCFR species (*e.g.* for Proteas (Midgley et al., 2003) and Rooibos tea (Lotter and le Maitre, 2014)). Range contractions are more likely to occur in narrow-ranged species, especially the climate-specialists, while wide-ranging species would probably experience a range expansion (Willis et al., 2010; Appendix Table S5.6). Species whose ranges are likely to contract are concentrated along the eastern and southwestern coastlines and escarpments (Fig. 5.5). Similar range expansion and contraction in 28 species of GCFR *Protea* were reported in the GCFR (Midgley et al., 2003).

According to the SDM predictions, *Thesium* suitable habitats, particularly around the southwest up to southeast, have been present since the LGM (Fig. 5.5). The exception was the Karoo Mountains and its fringes, which lacked suitable habitat during the LGM. However,

the habitat of some species, *e.g. T. whitehillensis*, persists and are projected to expand their distribution range in future (Fig. 5.5E). There was a strong negative relationship between the nature of range change between the LGM and the present, and of that between the present and 2080; implying a tendency for some species whose ranges have contracted since the LGM to expand in the future, and *vice versa*. With these fluctuations in range size over time, it can be deduced that some species respond negatively to change scenarios, while others benefit or are not affected.

With predicted future environmental change scenarios, the modelled range size of 51 species contracted (Fig. 5.5; Appendix Table S5.6). As such, climate change is a significant risk to the persistence of these species. At the global scale, several studies predict a substantial species range change due to rapid global warming *e.g.* Settele et al. (2014). At a local scale (the GCFR), the range extent of the Fynbos Biome is predicted to decline between 51% and 65% due to various climate scenarios (Lotter and le Maitre, 2014). With regional drying and warming, particularly in the western area, rainfall is projected to decline (Altwegg et al., 2014) and 23% of its species would probably be under extinction risk (Lotter and Maitre, 2014). Conversely, the 50 species with projected range maintenance or expansion are likely climate change tolerant species. The range expansion and contraction projected in this study corroborate with those reported for GCFR flora under different climate scenarios *e.g.* in *Diastella, Leucadendron, Leucospermum, Protea* and *Serruria* (Midgley et al., 2003), *Aspalathus* (Lotter and le Maitre, 2014) and the CFR endemic plants (Lenoir et al., 2008). However, these results should be interpreted cautiously given that the outcome might not represent immediate extinction (Midgley et al., 2003). Also, modelled range reduction, even from accurate data of environmental variables of species, is probabilistic (Midgley et al., 2003). More so, the model did not incorporate other Fynbos ecosystem functions such as fire regimes (typical of Fynbos dynamics, Cowling 1992). In cases such as fire, resprouters persist and regenerate after fire, but given the drier, hotter conditions that foster higher fire frequencies, climate change may prove problematic particularly to the reseeders (Cowling et al., 2015). In addition, land use has had a profound negative impact on habitat suitability in the GCFR flora (Raimondo et al., 2009). The GCFR *Thesium* species seldom occur on cultivated farmlands, residential areas or industrial sites (Zhigila, pers. obs). We hypothesize that the lack of occurrence in transformed sites could be linked to disruption of community dynamics, including the disruption of host-hemiparasite networks at criticall stages of establishments, on geographical distribution and ecology of *Thesium* species. In such scenarios, species could shift ranges to higher altitudes or rugged terrains where land use is limited (Midgley et al., 2003).

In the context of molecular phylogeny, we interrogated whether range extent, ecological specialisation and extinction risk are structured, and it was asked whether these will possibly impact *Thesium* phylogenetic diversity. Low phylogenetic signal was interpreted for variables with *K* and λ-values < 0.50, $p < 0.05$ for *K* and λ= 0 under random Brownian Motion of the evolutionary model for ecological specialisation and extinction risk in the GCFR *Thesium*. While *K* is suitable to modelling change in evolutionary rate, λ generally outperforms it in detecting phylogenetic signal (Münkemüller et al., 2012). In both cases, and in all variables, phylogenetic signal was close to zero (Fig. 5.6; Table 5.1), suggesting consistent random phylogenetic pattern. The low signal implies that climate change will not result in a disproportionate loss of *Thesium* phylogenetic diversity. This contrasts with the previous studies for example, Eiserhardt et al. (2015) and Willis et al. (2008). However, the labile phylogenetic structure observed might be due to evolutionary convergence in the deep nodes of the phylogenetic tree compared to individual lineages, which is often the case under a Brownian Motion model (Felsentein, 1985). The recent geographical and adaptive radiation among the GCFR *Thesium* lineages (Moore et al., 2010) is also a probable explanation for the low phylogenetic signal in the suite of ecological variables assessed in this study (Table 5.1). This agrees with the postulation of Davies et al. (2011) little or no loss of evolutionary pattern in lineages whose diversification rate was characterised by recent speciation particularly in biodiversity hotspots such as the GCFR.

In principle, species ecological specialisation and extinctions carry the signature of ecophysiological traits (Münkemüller et al., 2015; Liu et al., 2019). However, considering the extent of variations in the effect of phenotypic plasticity, phylogenetic signal derived from such traits might transcend to potential bias in their estimation. Previous studies *e.g.* Molina-Venegas and Rodríguez (2017), reported that polytomous chronograms might lead to an erroneous estimate of the phylogenetic signal. Ultimately, this may mislead the downstream facets, particularly the conservation strategy aspects (Davies et al., 2011). To overcome this probable error, the maximum clade credibility tree was used, which resolves polytomies in a phylogenetic tree given that Blomberg K models do not accept a polytomous tree (Blomberg and Garland, 2002; Blomberg et al., 2003) and the complementary use of Pagel's λ, which robustly handles even incompletely resolved phylogenies (Molina-Venegas and Rodríguez, 2017). Clearly, caution must be applied in the interpretation of a phylogenetic signal when evaluating environmental niches and extinction risk in the context of geospatial data (Zhang et al., 2017). However, when phylogenetic signal is consistently low, it implies there is a labile impact on phylogenetic diversity and species richness of the GCFR *Thesium*. Therefore, this

has limited contribution to the conservation planning of *Thesium* species.

What are the implications of the realised species geographical extents for conservation of the GCFR *Thesium*? Of the 65 species currently ranked as Least Concern or Data Deficient on the South African Red list, the data show that 24 species will likely shift into higher extinction risks. The South African National strategy has flagged *Thesium* as a priority plant taxon for taxonomic and conservation study (Victor et al., 2015), as nearly 30% of the species have uncertain conservation status and are likely to be threatened (Raimondo et al., 2009; Von Staden, 2015). For effective conservation planning, it is necessary to understand the distribution ranges of species and their relationship with abiotic and other biotic variables (Mokany and Ferrier, 2011; Soultan et al., 2019). Our findings present several important outcomes for the local and regional conservation planning of *Thesium* and as a proxy to other GCFR biota. As is the case in most GCFR plant species (Midgley et al., 2003; Davies et al., 2011), most *Thesium* evolutionary events occurred recently (Moore et al., 2010), implying that the current distribution patterns of extant *Thesium* was shaped by relatively recent glacial events. This suggests that the GCFR is a key region in the diversification history of *Thesium* and therefore deserves to be prioritized when making a conservation decision at local or on a global scale.

Range-restricted species have been shown to be more vulnerable to range loss than wide-ranged species (Davies et al., 2011; Yessoufou et al., 2012). Since ecological specialists are mostly endemics, any extinction drivers associated with these species conveys a significant probability in the loss of important global biodiversity. Therefore, a high concentration of specialists and by implication endemics in each biome implies that many species will be affected in the event of any single threat (Raimondo et al., 2009). The data from this study provide corroborative evidence for vulnerability of ecological specialists to range loss and possible threats. Although limited on *Thesium*, the extirpation of range-restricted ecological specialists from a biome may impact on the phylogenetic diversity, pruning the tree of life (Vamosi et al., 2014; Eiserhardt et al., 2015) and ultimately affecting the stability of the operational ecosystem (Clavel et al., 2011). Therefore, narrow-ranged species are worth conservation priority. Also, identifying threatened habitats with a high concentration of ecological specialists and making decisive efforts to reserve them is an important conservation action that should be taken.

## 5.5 Conclusion

The GCFR is the center of *Thesium* diversity, but the driving factors behind this taxon's rapid diversification and distribution are poorly understood. In the context of the GIS data used in this study, it was confirmed that the GCFR *Thesium* consists of both ecological specialists and generalists and best epitomizes the correlates of the extinction rate faced by narrow-ranged species due to rapid climate change. The results indicate that the ecological specialism, range extent and extinction risk of species are positively correlated. However, the species distribution models show a negative relationship between species range change responses from the LGM to present and from the present to 2080. In other words, ca. 50% of species whose ranges have increased since the LGM are predicted to suffer a decline in range in future, implying a conservation concern. Contrastingly, 44% of the GCFR *Thesium* species are expected to expand their ranges in the face of climate change, which perhaps suggests a limited concern for conservation planning. Phylogenetic signal analyses show that local environmental breadths and extinction risk are phylogenetically low, with closely related lineages occupying habitat that are more similar than expected by random chance. The lack of signal implies that climate change will not result in a disproportionate loss of *Thesium* phylogenetic diversity, which contrasts with the findings of previous studies *e.g.*, Eiserhardt et al. (2015) and Willis et al. (2003) on *Plectranthus*. Therefore, this suggests that the phylogenetic signal in the distribution ranges of *Thesium* species are negligible and might not be a reliable guide to infer a clades' habitat preferences.

# CHAPTER SIX

## 6. SYNTHESIS

Prior to this study, *Thesium* was listed among priority genera for taxonomic studies (Victor et al., 2015). The last revision of the entire genus was done by De Candolle in 1857 and the southern African taxa was last revised by Hill in 1925. Currently, the classification adopted by Hill (1925) provides an artificial system with little predictability regarding species delimitation. Clearly, there was an urgent need for an updated classification system that incorporates multiple lines of evidence, particularly in the context of modern taxonomy. Moore et al. (2010) initiated this by studying the molecular component of the relationship of species in *Thesium*, but his work included incomplete taxon sampling and was based on only two loci (ITS and trnL-F). A much-expanded taxon and loci sampling was required, and this needed to be integrated with biogeography and morphology in order to untangle these relationships in a more meaningful and predictive way.

The first aim of thesis (Chapter 2) was to test the monophyly of the genus *Thesium* relative to the segregate taxa *Thesidium, Chrysothesium, Kunkeliella* and *Austroamericium* (Moore et al., 2010; Nickrent and García, 2015) and to develop a robust phylogeny upon which infrageneric/sectional classification framework could be formulated. In addition, morphological synapomorphies needed to be identified for each clade. I found the phylogenetic relationships in *Thesium* to be broadly congruent with previous hypotheses (Moore et al., 2010; Nickrent and García et al., 2015; García et al., 2018), but with increased support values due to the expanded DNA loci and taxon sampling. *Thesium* is monophyletic, and the inclusion of the segregate genera (listed above) supports their synonymization into *Thesium* by Forest and Manning (2013). Within the genus *Thesium*, the new infrageneric classification scheme proposed in this study recognized the establishment of five monophyletic clades as subgenera: *Hagnothesium* (8 species, the GCFR endemics), *Thesium* (64 species, Eurasian), *Discothesium* (13 species, South African), *Psilothesium* (101 species, Tropical/subtropical) and *Frisea* (103 species, South African) following nomenclatural rules (Shenzeng Code; Turland et al., 2018). To aid identification and diagnosis, I presented a taxonomic key to the subgenera and provided a taxonomic circumscription for each subgenus. The diagnosis of each subgenus was based on the ancestral morphological character reconstructions, which identified either synapomorphies, symplesiomorphies or homoplasies for each clade (Zhigila et al., 2020).

Informed by the monophyly of each clade, I have in the context of this study opted to revise clade 1 (subgenus *Hagnothesium*) as a starting point toward revising of the whole genus (Zhigila et al., 2019a). *Hagnothesium,* comprising species entirely endemic to the Greater Cape Florisic Region (GCFR) GCFR in South Africa (Manning and Goldblatt, 2012; Von Staden, 2015), is a data deficient taxon and recently considered as a taxonomically problematic and complex group in terms of species delimitation (Forest and Manning, 2013). Therefore, a reassessment of species boundaries was conducted of subgenus *Hagnothesium*: measuring a range of morphological traits (floral, fruit and vegetative) on a representative set of specimens (wherever possible, n = 15) and ultrastructural traits of each species. These measurements were then subjected to standard univariate and multivariate morphometric approaches to identifying species boundaries. Of the 15 names listed in this clade (previously called *Thesidium,* SANBI, 2015; The Plant List, 2018), this study recognized eight distinct species (*T. fragile, T. fruticulosum, T. hirtum, T. leptostachyum, T. longicaule, T. microcarpum, T. minus* and *T. quartzicolum*), with *T. quartzicolum* newly described here.

A further six taxa new to science were discovered during fieldwork for this study and are described as part of this study. For species delimitation, the unified species concept (de Queiroz, 2007), which is an integrative approach that utilizes several lines of taxonomic evidence to recognize distinct species (Leaché et al., 2009; Victor et al., 2016; Sukumaran and Knowles, 2017; Noguerales et al., 2018) was adopted to describe these novel collections. These are *Thesium aspermontanum, T. dmmagiae, T. neoprostratum, T. nigroperianthum, T. rhizomatum* and *T. stirtonii.* Also, *T. sawae* was elevated to species from *T. assimile* A.DC. var. *pallidum* A.DC. (Zhigila et al., 2019b). Four of the new species *T. dmmagiae, T. nigroperianthum, T. rhizomatum* and *T. stirtonii* were collected from the Overberg in highly heterogenous habitats, which have also been a source of several other recently described species (Curtis et al., 2013). Except for *T. stirtonii* (which was collected and deposited in the herbaria as *T. nigromontanum*), these taxa were recently collected from the field survey as part of this study. The hypothesis by Treurnicht et al. (2017) that 99% of the CFR plant species have been described seems encouraging, but the recognition of these new species implies that a greater percentage of species within the CFR might have not yet have been described. Morphological and ecological differences between each new species and their putative closest affinities, preliminary conservation status, phenology and distributional maps are presented in chapter four.

The diversity of living organisms is hypothetically driven by three main factors, biotic (other interacting organisms), abiotic (environmental variables) and migration (in case of animals) or dispersal (for plants) (the BAM concept; Pearson and Dawson, 2003; Soberón, 2007; Soberón & Nakamura 2009). These factors are predicted to shape the ranges in which species are distributed (Barbosa et al., 2012; Beale et al., 2014). In this study, I evaluated the role of environmental variables (climate, soil, elevation) in driving the ranges of GCFR *Thesium* species ranges (wide versus narrow), and their correlation with extinction risks under varied climatic scenarios. Also, I assessed whether variation in range size, ecological specialisation and extinction proneness arephylogenetically structured. This revealed a strong positive linear correlation between species-specific elevation, climate, soil and their respective niche breadths. The species habitat suitability model showed that *Thesium* species will respond to climate change through range expansion and/or contraction with pronounced range loss associated with climate specialists. Interestingly, several generalists and/or habitat specialists seem to benefit from the impacts of climate change given that their range size increased over time. Regrettably, there is a projected increase in imperiled species in the assessments of the extent of occurrence in the face of climate scenarios projected for the year 2080. However, the test for phylogenetic signal indicated random phylogenetic clustering for both species ecological specialisation and extinction risk, thereby suggesting a labile impact on the phylogenetic diversity of the GCFR *Thesium*.

Overall, this thesis contributes to the understudied genus *Thesium.* The knowledge thus generated can be extrapolated to the systematics, evolution and biogeography of other plant taxa, particularly those in the GCFR. The seven new species described add to the understanding of biodiversity catalogue. Also, the reassessment of conservation status of *Thesium* species provides valuable information for guiding conservation practices.

**REFERENCES**


Aldhebiani, A.Y., 2018. Species concept and speciation. *Saudi Journal of Biological Sciences* 25:437–440.

Allsopp, N., Colville, J.F., Verboom, G.A. and Cowling, R.M. 2014. Fynbos: Ecology, Evolution, and Conservation of a Megadiverse Region. Oxford University Press. Pp. 119 – 140. Statsoft.com. (2016).

Allsopp, N. 2016. South African Environmental Observation Network: *Fynbos Node Science Plan:* 2016–2018.

Altwegg, R., West, A., Gillson, L. and Midgley, G.F. 2014. Impacts of climate change in the Greater Cape Floristic Region. In Fynbos: Ecology, Evolution, and Conservation of a Megadiverse Region. Oxord University Press, London.

Andersson, L. 1990. The driving force: Species concepts and ecology. *Taxon* 39:375–382.

Araújo, M.B., Alagador, D., Cabeza, M. Nogues-Bravo, D. and Thuiller, W. 2011. Climate change threatens European conservation areas. *Ecology Letters* 14:484–492.

ArcGIS Desktop version 10.6.1, 2018. Redlands, CA: Environmental Systems Research Institute.

Bachman, S., Moat, J., Hill, A.W., De la Torre, J. and Scott, B. 2011. Supporting Red List threat assessments with GeoCAT: geospatial conservation assessment tool. *ZooKeys* 150:117–126.

Backlund, A. and Bremer, K. 1998. To be or not to be: Principles of classification and monotypic plant families. *Taxon* 47:391–400.

Barbosa, F.G., Schneck, F. and Melo, A.S. 2012. Use of ecological niche models to predict the distribution of invasive species: a scientometric analysis. *Brazilian Journal of Biology = Revista Brasileira de Biologia* 72(4):821–829.

Barrett, S.C.H. 2013. The evolution of plant reproductive systems: how often are transitions irreversible? *Proceedings of the Royal Society B: Biological Sciences* 280: 289.

Beale, C.M., Brewer, M.J. and Lennon, J.J. 2014. A new statistical framework for the quantification of covariate associations with species distributions. *Methods in Ecology and Evolution* 5:421–432.

Bergh, N.G., Verboom, G.A., Rouget, M. and Cowling, R.M. 2014. Vegetation types of the Greater Cape Floristic Region. In Allsop, N., Colville, J.F., Verboom, G.A. and Cowling, R.M. 2014. Fynbos: Ecology, Evolution, and Conservation of a Megadiverse Region. Oxford University Press. Pp. 1– 25.

Bergius, J.P. 1767. Descriptiones Plantarum ex Capite Bonae Spei. Pg. 73

Blomberg, S.P. and Garland, T. 2002. Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. *Journal of Evolutionary Biology* 15:899–910.

Blomberg, S.P., Garland, T. and Ives, A.R. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* 57:717–745.

Bobrov, E. G. 1936. Santalaceae. *Flora of the USSR*, Moscow. Pg. 412–431.

Bond, W. and van Wilgen, B., 1996. Fire and Plants. Chapman and Hall, London, pp. 227.

Boria, R. A., Olson, L. E., Goodman, S. M and Anderson, R. P. 2014. Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecology Models* 275:73–77.

Born, J., Linder, H.P. and Desmet, P. 2007. The Greater Cape Floristic Region. *Journal of Biogeography* 34:147–162.

Botts, E.A., Erasmus, B.F.N. and Alexander, G.J. 2013. Small range size and narrow niche breadth predict range contractions in South African frogs. *Global Ecology and Biogeography* 22:567–576.

Bouckaert R., Vaughan T.G., Barido-Sottani J., Duchêne S., Fourment M., Gavryushkina A. 2019. BEAST 2.5: An advanced software platform for Bayesian evolutionary analysis. *PLoS Computational Biology* 15(4):1006650.

Bradshaw, P.L. and Cowling, R.M., 2014. Landscapes, rock types, and climate of the Greater Cape Floristic Region in Fynbos: Ecology, Evolution, and Conservation of a Megadiverse Region, Oxford University Press, USA. Pg. 26–46.

Breiner, F.T. Guisan, A., Nobis, M.P. and Bergamini, A. 2017. Including environmental niche information to improve IUCN Red List assessments. *Diversity and Distributions* 23:484–495.

Brenan, J.P.M. 1979. Three new species of *Thesium* (Santalaceae) from South Africa. *Kew Bulletin* 33(3):395–397. www.jstor.org/stable/4110134

Brennan, H. 2013. Ecological Specialization. Retrieved Aug 25, 2019 from Explorable.com: https://explorable.com/ecological-specializatio

Brown, N.E. 1932. *Thesium*. In: Davy, J.B. (Ed.) A manual of the flowering plants and ferns of the Transvaal with Swaziland, South Africa. Longmans, Green and Company, London. Pg. 455–462.

Brummitt, R.K. 2001. World Geographical Scheme for Recording Plant Distributions: Edition 2. International Working Group on Taxonomic Databases for Plant Sciences (TDWG). Archived from the original on 2016-01-25. Retrieved 2016-04-06.

Burgman, M.A. and Fox, J.C. 2003. Bias in species range estimates from minimum convex

polygons: implications for conservation and options for improved planning. *Animal Conservation* 6:19–28.

Cardillo, M. and Meijaard, E. 2012. Are comparative studies of extinction risk useful for conservation? *Trends in Ecology and Evolution* 27:167–71.

Chandler, G.T. and Crisp, M.D. 1998. Morphometric and phylogenetic analysis of the *Daviesia ulicifolia* complex (Fabaceae, Mirbelieae) *Plant Systematics and Evolution* 209:93–122.

Chase, B.M. and Meadows, M.E. 2007. Late Quaternary dynamics of southern Africa's winter rainfall zone. *Earth-Science Reviews* 84:103–138.

Chen, Z.-Q. and Benton, M.J. 2012. The timing and pattern of biotic recovery following the end-Permian mass extinction. *Nature Geoscience* 5:375–383.

Chivers, C., Leung, B. and Yan, N.D. 2014. Validation and calibration of probabilistic predictions in ecology. *Methods in Ecology and Evolution* 5:1023–1032.

ChromasPro version 2.1.5., 2017. Technelysium Pty Ltd, South Brisbane, Queens and Australia.

Clark, D. A. 2007. Detecting tropical forests' responses to global climatic and atmospheric change: Current challenges and a way forward. *Biotropica* 39:4.

Clavel, J., Julliard, R. and Devictor, V. 2011. Worldwide decline of specialist species: toward a global functional homogenization? *Frontiers in Ecology and the Environment* 9:222–228.

Compton, R.H. 1931. The flora of the Whitehill District. *Transactions of the Royal Society of South Africa* 19(3):269–326.

Condamine, F.L., Rolland, J. and Morlon, H. 2013. Macroevolutionary perspectives to environmental change. *Ecology Letters* 16:72–85.

Cooper, N., Bielby, J., Thomas, G.H. and Purvis, A. 2008. Macroecology and extinction risk correlates of frogs. *Global Ecology and Biogeography* 17:211–221.

Cope, J.S., Corney, D., Clark, J.Y., Remagnino, P. and Wilkin, P. 2012. Plant species identification using digital morphometrics: A review. *Expert Systems with Applications* 39:7562–7573.

Cowling, R.M. 1992. The Ecology of Fynbos: Nutrients, Fire and Diversity. Oxford University Press, Cape Town.

Cowling, R.M. and Lombard, A.T. 2002. Heterogeneity, speciation/extinction history and climate: explaining regional plant diversity patterns in the Cape Floristic Region. *Diversity and Distributions* 8:163–179

Cowling, R.M., Potts, A.J., Bradshaw, P.L., Colville, J., Arianoutsou, M., Ferrier, S., Forest,

F., Fyllas, N.M., Hopper, S.D., Ojeda, F., Procheş, Ş., Smith, R.J., Rundel, P.W., Vassilakis, E. and Zutta, B.R. 2015. Variation in plant diversity in Mediterranean-climate ecosystems: the role of climatic and topographical stability. *Journal of Biogeography* 42:552–564.

Cramer, M.D., West, A.G., Power, S.C., Skelton, R. and Stock, W.D. 2014. Plant ecophysiological diversity in Fynbos: Ecology, Evolution, and Conservation of a Megadiverse Region. Oxford University Press. Pg. 248–272.

Cramer, M.D., Wootton, L.M., van Mazijk, R. and Verboom, G.A. 2019. New regionally modelled soil layers improve prediction of vegetation type relative to that based on global soil models. *Diversity and Distributions* 25:1736–1750.

Curtis, O.E., Stirton, C.H. and Muasya, A.M. 2013. A conservation and floristic assessment of poorly known species rich quartz-silcrete outcrops within Rûens Shale Renosterveld (Overberg, Western Cape), with taxonomic descriptions of five new species. *South African Journal of Botany* 87:99–111.

Darriba D., Taboada G.L., Doallo, R. and Posada, D. 2012. "jModelTest 2: more models, new heuristics and parallel computing". *Nature Methods* 9(8):772

Darriba, D., Posada, D., Kozlov, A.M., Stamatakis, A., Morel, B. and Flouri, T. 2019. ModelTest-NG: a new and scalable tool for the selection of DNA and protein evolutionary models, *Molecular Biology and Evolution* 13(55):1–6.

Davies, T.J., Smith, G.F., Bellstedt, D.U., Boatwright, J.S., Bytebier, B., Cowling, R.M., Forest, F., Harmon, L.J., Muasya, A.M., Schrire, B.D., Steenkamp, Y., van der Bank, M., Savolainen, V. 2011. Extinction risk and diversification are linked in a plant biodiversity hotspot. *PLoS Biology* 9(5):1000620.

Dayrat B. 2005. Towards integrative taxonomy. *Biological Journal of the Linnaean Society* 85: 407–415.

De Candolle, A. 1857a. Santalaceae. In: De Candolle, A. (Ed.), *Prodromus systematis naturalis*, Vol. 14. Treuttel and Würtz, Paris Pg. 619–692.

De Candolle, A. 1857b. *Espéces nouvelles du genre* Thesium *présentées à la Société de physique et d'Histoire Naturelle de Genève dans sa séance du 25 Mai 1857*. Ramboz and Schuchardt, Genève. Pg. 1–8.

De Queiroz, K. 2007. Species concepts and species delimitation. *Systematic Biology* 56(6):879–886.

Der, J. P., and Nickrent, D. L. 2008. A molecular phylogeny of Santalaceae (Santalales). *Systematic Botany* 33:107–116.

Devictor, V., Clavel, J., Julliard, R., Lavergne, S., Mouillot, D., Thuiller, W., Venail, P., Villéger, S. and Mouquet, N. 2010. Defining and measuring ecological specialization. *Journal of Applied Ecology* 47:15–25.

Devictor, V., Julliard, R., and Jiguet, F. 2008. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos* 117:507–514.

Dexter, K.G., Terborgh, J.W. and Cunningham, C.W. 2012. Historical effects on beta diversity and community assembly in Amazonian trees. *Proceedings of the National Academy of Sciences USA* 109:7787–7792.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D. and Lautenbach, S. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36:027–046.

Doyle, J.J. and Doyle, J.L. 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochemical Bulletin of the Botanical Society of America* 19:11–15.

Dubuis, A., Giovanettina, S., Pellissier, L., Pottier, J., Vittoz, P. and Guisan, A. 2013. Improving the prediction of plant species distribution and community composition by adding edaphic to topo-climatic variables. *Journal of Vegetation Science* 24:593–606

Duminil, J., Kenfack, D., Viscosi, V., Grumiau, L. and Hardy, O.J. 2012. Testing species delimitation in sympatric species complexes: The case of an African tropical tree, *Carapa* spp. (Meliaceae). *Molecular Phylogenetics and Evolution* 62:275–285.

Elith, J. and Leathwick, J.R. 2009. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annual Review of Ecology, Evolution, and Systematics* 40:677–97.

Elith, J., Phillips, S.J., Hastie, T., Dudık, M., Chee, Y.E. and Yates, C.J. 2011. A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* 17:43–57.

Felsenstein, J. 1985. Phylogenies and the comparative method. *The American Naturalist* 125:1–15.

Everitt, B.S., Leese, S.B.L.M. and Stahl, D. 2011. Cluster Analysis. 5th ed. King's College London, UK. Pg. 324–326.

Feng, X., Park, D.S., Ye Liang, Y., Pandey, R. and Papeş, M. 2019. Collinearity in ecological niche modeling: Confusions and challenges. *Ecology and Evolution* 00:1–12.

Fielding, A.H. and Bell, J.F. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24:38e49.

Forest, F. and Manning, J.C. 2013. The minor genera *Kunkeliella* and *Thesidium* included in *Thesium*. *Bothalia* 43(2):214–216.

García, M.A., Nickrent, D.L. and Mucina, L. 2018. *Thesium nautimontanum*, a new species of Thesiaceae (Santalales) from South Africa. *PhytoKeys* 109:41–51.

GBIF (Global Biodiversity Information Facility) 2019. https://www.gbif.org/en/, accessed 12/03/2019.

GeoCAT, 2018. http://geocat.kew.org/editor#/add-points. (Accessed 13/10/2018).

Germishuizen, G., Meyer, N., Steenkamp, Y. and Keith, M. 2006. A checklist of South African plants. *South African botanical diversity network report no. 41*. SABONET, Pretoria. Pg. 767–772.

Goldblatt, P. 1978. An analysis of the flora of Southern Africa: its characteristics, relationships, and origins. *Annals of the Missouri Botanical Garden* 65:369–436.

Goldblatt, P. and Manning, J. 2000. Cape Plants: a conspectus of the Cape flora of South Africa. National Botanical Institute, Cape Town.

Gorb, E. and Gorb, S. 2003. Seed Dispersal by Ants in a Deciduous Ecosystem. Kluwer Academic Publishers, Dordrecht, the Netherlands.

Gower, J. C. 1971. A general coefficient of similarity and some of its properties. *Biometrics* 27:857–874.

Grandcolas, P., Nattier, R., Legendre, F. and Pellens, R. 2011. Mapping extrinsic traits such as extinction risks or modelled bioclimatic niches on phylogenies: does it make sense at all? *Cladistics* 27:181–185.

Grismer, L.L. 2001. An evolutionary classification and checklist of amphibians and reptiles on the Pacific islands of Baja California, Mexico. *Bulletin of the Southern California Academy of Science* 100:12–23.

Gudžinskas, Z. and Žalneravičius, E. 2017. Notes on the enigmatic *Thesium linophyllon* and report on *Thesium ramosum* in Lithuania. *Botanica Lithuanica* 23(2):111–122.

Guisan, A. and Thuiller, W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecological Letters* 8:993-1009.

Guisan, A. and Zimmermann, N.E. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135:147–186.

Hall, T.A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposiun Series* 41:95–98.

Hammer, Ø., Harper, D. A.T. and Ryan, P.D. 2001. PAST: Paleontological Statistics Software Package for Education andData Analysis. *Palaeontologia Electronica* 4(1):4–9.

Hammond, T.T., Palme, R. and Lacey, E.A. 2018. Ecological specialization, variability in activity patterns and response to environmental change. *Biology Letters* 14:20180115.

Hannah, L., Midgley, G.F., Hughes, G. and Bomhard, S. 2005. The view from the Cape: extinction risk, protected areas, and climate change. *Bioscience* 55:231–242.

Harbaugh, D. T. and Baldwin, B. G. 2007. Phylogeny and biogeography of the sandalwoods (*Santalum*, Santalaceae): repeated dispersals throughout the Pacific. *American Journal of Botany* 94:1028–1040.

Harbaugh, D.T. 2008. Taxonomic Revision of the Endangered Hawaiian Red-flowered Sandalwoods (*Santalum*) and Discovery of an Ancient Hybrid Species. *Systematic Botany* 35(4):827–838.

Harmon, L.J., Weir, J., Brock, C., Glor, R.E., Challenger, W., Hunt, G., FitzJohn, R., Pennell, M.W., Slater, G.J., Brown, J.W., Uyeda, J., and Eastman., J.M. 2019. Analysis of Evolutionary Diversification using Geiger package, Version 2.0.6.2

Harrison, S. and Noss, R. 2017. Endemism hotspots are linked to stable climatic refugia. *Annals of Botany* 119: 207–214.

Hendrych, R. 1963. *Austroamericium* genero nuevo (Santalaceae). *Boletim Sociedade Argentina Botanico* 10:120–128.

Hendrych, R. 1972. The natural history and systematic of the genus *Thesium* L. *Acta Universitatis Carolinae - Biologica* 1970: 293–358.

Hendrych, R. 1994. *Chrysothesium*, eine neue Gattung in der Familie Santalaceae. *Preslia* 65:311–324.

Hernandez, P. A., Graham, C. H., Master, L. L. and Albert, D. L. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* 29:773–785.

Hernderson, A. 2006. Traditional morphometrics in plant systematics and its role in palm systematic. *Botanical Journal of the Linnean Society* 151:103–111.

Hieronymus, G. 1889. Santalaceae. Pages 202–227 in A. Engler and K. Prantl, eds. Die Naturlichen. Pflanzenfamilien, Leipzig.

Hijmans, R.J. 2017. Introduction to the 'raster' package (version 2.6-7). R package.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. and Jarvis, A. 2005. Very highly resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25(15):1965–1978.

Hill, A.W. 1915a. The genus *Thesium* in South Africa, with a key and descriptions of new species. *Bulletin of Miscellaneous Information Kew* 1: 1–43.

Hill, A.W. 1915b. Notes on South African Santalaceae, Thesidium. *Bulletin of Miscellaneous Information Kew* 3:97–99.

Hill, A.W. 1925. Order CXX. Santalaceae. In: Thiselton-Dyer, W.T. (Ed.), *Flora Capensis*, Vol. 5. L. Reeve and Co. Ltd., London. Pg. 135–212.

Hilliard, O.M. 1991**.** New names in *Thesium* (Santalaceae) from the Flora Zambesiaca area. *Edinburgh Journal of Botany* 48:53–54.

Hilliard, O.M. 2004. Santalaceae *Flora Zambesiaca* 9(3):1–13.

Hitchcock, A.S. 1929. International Botanic Congress, Cambridge, England, 1930, Proposals by British Botanists: Pg. 135.

Humphreys, A.M. and Linder, H.P. 2009. Concept versus data in delimitation of plant genera. *Taxon* 58:1054–1074.

Hutchinson, J., Dalziel, J.M., Keay, R.W.J. and Hepper, N. 2014. Flora of West Tropical Africa. eBook. Downloaded from OpenLibrary.org.

Hyde, M.A., Wursten, B.T., Ballings, P. and Palgrave, C.M. 2017**.** *Flora of Zimbabwe: Genus page: Thesium.* http://www.zimbabweflora.co.zw/speciesdata/genus.php.

Iloh, A.C. and Ogundipe, O.T. 2016. Using ecological niche models to plan conservation in a changing environment: A case for the plant Chasmanthera dependens Hochst (Menispermaceae) in West Africa. *Journal of Ecology and the Natural Environment* 8(1): 1–8.

IUCN 2017. *Guidelines for using the IUCN Red List categories and criteria*. Version 12. Standards and Petitions Subcommittee. http://www.iucnredlist.org/documents/RedListGuidelines.pdf (Accessed in January 2019).

Jaubert, H.F. and Spach, E. 1844. Illustrationes plantarum orientalium, Paris**.**

JSTOR 2019 https://plants.jstor.org/compilation/ (Accessed on 28/02/2019).

Judd, W.S., Campbell, C.S., Kellogg, E.A., Stevens, P.F. and Donoghue, M.J. 2012. Plant systematics: A phylogenetic approach, 3rd ed. Sinauer Associates, Inc. USA, 104.

Júnior, D.P. and No´brega, C.C. 2018. Evaluating collinearity effects on species distribution models: An approach based on virtual species simulation. *PLoS ONE* 13(9):e0202403.

Katoh, K., Rozewicki, J. and Yamada, K.D. 2017. MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Briefings in Bioinformatics* 1–7.

Keck, F. 2019. Phylosignal: Exploring the Phylogenetic Signal in Continuous Traits.

Kelly, S., Grenyer, R. and Scotland, R.W. 2014. Phylogenetic trees do not reliably predict trait

diversity. *Diversity & Distribution* 20:600–612.

Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., Blomberg, S.P. and Webb, C.O. 2010. Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26:1463–1464.

Keppel, G., Robinson, T., Wardell-Johnson, G.W. 2017. Low-altitude mountains as refugium for two narrow endemics in the Southwest Australian Floristic Region biodiversity hotspot. *Annals of Botany* 119:289–300.

Kier, G. and Barthlott, W. 2001. Measuring and mapping endemism and species richness: a new methodological approach and its application on the flora of Africa. *Biodiversity and Conservation* 10:1513–1529.

Kotze, D.J. and O'Hara, R.B. 2003. Species decline – but why? Explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe. *Oecologia* 135:138–148.

Koutecký, P., 2015. MorphoTools: a set of R functions for morphometric analysis. *Plant Systematics and Evolution* 301:1115–1121.

Kremen, C., Cameron, A., Moilanen, A., Phillips, S.J., Thomas, C.D., Beentje, H., Dransfield, J., Fisher, B.L., Glaw, F., Good, T.C., Harper, G.J., Hijmans, R.J., Lees, D.C., Louis ., E., Jr, Nussbaum, R.A., Raxworthy, C.J., Razafimpahanana, A., Schatz, G.E., Vences, M., Vieites, D.R., Wright, P.C. and Zjhra, M.L. 2007. Aligning conservation priorities across taxa in Madagascar with high-resolution planning tools. *Science* 320:222–226.

Kuntze, O. 1904. Lexicon generum phanerogamarum, Stuttgart.

Kuraku, S., Zmasek, C.M., Nishimura, O. and Katoh, K. 2013. aLeaves facilitates on-demand exploration of metazoan gene family trees on MAFFT sequence alignment server with enhanced interactivity. *Nucleic Acids Research* 41:W22–28.

Kuzmina, M.L., Johnson, K.L., Barron, H.R. and Herbert, P.D.N. 2012. Identification of vascular plants of Churchill, Manitoba, using a DNA barcode library. *BMC Ecology* 12:1–11.

Lawalrée, A. 1985. Especes nouvelles d'Afrique centrale du genre *Thesium* L. sous-section *Fimbriata* A.W.Hill (Santalaceae). *Bulletin Jardin Botanica Nacionale Belgium* 55:17–25.

Leaché, A.D., Koo, M.S., Spencer, C.L., Papenfuss, T.J., Fisher, R.N. and McGuire, J.A. 2009. Quantifying ecological, morphological, and genetic variation to delimit species in the coast horned lizard species complex (Phrynosoma). *Proceedings of the National Academy of Sciences of the United States of America* 106(30):12418–12423.

Leister, O.A. and Morris, J.W. 1976. South African place names. *Annals of the Cape Provincial*

*London* 5(2):135–200.

Lenoir, J., Gegout, J.C., Marquet, P.A., de Ruffray, P. and Brisse, H. 2008. A significant upward shift in plant species optimum elevation during the 20th century. *Science* 320:1768–1771.

Levyns, M.R. 1950. Two new species of *Thesium* and some notes on other species. *Journal of South African Botany* 6:73–78.

Linnaeus, C. 1753. *Species plantarum*: exhibentes plantas rite cognitas ad genera relatas cum differentiis specificis nominibus trivialibus, synonymis selectis, locis natalibus, secundum systema sexuale digestas. Holmiæ: Impensis Laurentii Salvii.

Linnaeus, C.f. 1782. Supplementarum plantarum. Braunshweig.

Lirio, E.J., Peixoto, A.L. and Siqueira, M.F. 2015. Taxonomy, conservation, geographic and potential distribution of Macrotorus Perkins (Mollinedioideae, Monimiaceae), and a key to the Neotropical genera of Monimiaceae. *Phytotaxa* 234:201–214.

Liu, C., Li, X., Cheng, R., Han, Z., Yang, L., Song, Z. and Wang, Z. 2018. Anti-oral common pathogenic bacterial active acetylenic acids from Thesium chinense Turcz. *Journal of Natural Medicines* 72:433–438.

Lombard, N.V., Le Roux, M.M. and van Wyk, B.E. 2019. *Thesium ovatifolium* (Santalaceae), a new species with ovate leaves from KwaZulu-Natal, South Africa. *Phytotaxa* 405(5):263–268.

Lotter, D. and le Maitre, D. 2014. Modelling the distribution of *Aspalathus linearis* (Rooibos tea): implications of climate change for livelihoods dependent on both cultivation and harvesting from the wild. *Ecology and Evolution* 4(8):1209–122.

Lourenço-de-Moraes, R., Lansac-Toha, F.M., Schwind, L.T.F., Arrieira, R.L., Rosa, R.R., Terribile, L.C., Lemes, P., Range, T.F., Diniz-Filho, J.A.F., Bastos, R.P. and Bailly, D. 2019. Climate change will decrease the range size of snake species under negligible protection in the Brazilian Atlantic Forest hotspot. *Scientific Reports* 9:8523.

Lozier J.D., Aniello, P. and Hickerson, M.J. 2009. Predicting the distribution of Sasquatch in western North America: anything goes with ecological niche modeling. *Journal of Biogeography (J. Biogeogr.)* 36:1623–1627.

Maddison, W.P., and Maddison, D.R. 2018. Mesquite: a modular system for evolutionary analysis. mesquiteproject.org/mesquite/mesquite.html

Manning, J. and Goldblatt, P. 2012. Plant of the Greater Cape Floristic Region 1: The Core Cape Flora, *Strelitzia* 29. South African National Biodiversity Institute, Pretoria Pg. 724–729.

Mashego, K.S. and Le Roux, M.M. 2018. A taxonomic evaluation of the *Thesium confine* species complex (Santalaceae). *Bothalia* 48(1):a2346.

Merriam-Webster, 2019. Accessed August 9, 2019, from https://www.merriam-webster.com/dictionary/hacker.

Midgley, G.F., Hannah, L., Millara, D., Thuiller, W. and Booth, A. 2003. Developing regional and species-level assessments of climate change impacts on biodiversity in the Cape Floristic Region. *Biological Conservation* 112:87–97.

Miller, A. G. 1989. Santalaceae. Pages 379-381 in I. Hedberg and I. S. Edwards, eds. Flora Ethiopia, Addis Ababa and Asmara (Ethiopia), Uppsala (Sweden).

Miller, M.A., Pfeiffer, W., and Schwartz, T. 2010 "Creating the CIPRES Science Gateway for inference of large phylogenetic trees" in Proceedings of the Gateway Computing Environments Workshop (GCE), Nov. 2010, New Orleans, LA Pg. 1–8.

Mitchell, N., Lewis, P.O., Lemmon, E.M., Lemmon, A.R. and Holsinger, K.E. 2017. Anchored phylogenomics improves the resolution of evolutionary relationships in the rapid radiation of Protea L. *American Journal of Botany*, 104(1):1–14.

Moat, J., Bachman, S.P., Field, R. and Doreen S. Boyd, D.S. 2018. Refining area of occupancy to address the modifiable areal unit problem in ecology and conservation. *Conservation Biology* 32(6):1278–1289.

Mokany, K. and Ferrier, S. 2011. Predicting impacts of climate change on biodiversity: a role for semi-mechanistic community-level modelling. *Diversity & Distribution* 17:374–380.

Molina-Venegas, R. and Rodríguez, M.A. 2017. Revisiting phylogenetic signal; strong or negligible impacts of polytomies and branch length information? BMC Evolutionary Biology 17:53.

Moore, T.E., Verboom, A.G. and Forest, F. 2010. Phylogenetics and biogeography of the parasitic genus *Thesium* L. (Santalaceae), with an emphasis on the Cape of South Africa. *Botanical Journal of the Linnaean Society* 162:435–452..

Mora, C. and Sale, P. 2011. Ongoing global biodiversity loss and the need to move beyond protected areas: a review of the technical and practical shortcomings of protected areas on land and sea. *Marine Ecology Progress Series* 434:251–266.

Morelli, F., Benedetti, Y., Møller, A.P. and Fuller, R.A. 2019. Measuring avian specialization. *Ecology and Evolution* 00:1–9.

Morueta-Holme, N., Enquist, B.J., McGill, B.J. Boyle, B., Jørgensen, P.M., Ott, J.E., Peet, R.K., Sımova, I., Sloat, L.L., Thiers, B., Violle, C., Wiser, S.K., Dolins, S., Donoghue, J.C., Kraft, N.J.B., Regetz, J., Schildhauer, M., Spencer, N. and Svenning, J. 2013. Habitat

area and climate stability determine geographical variation in plant species range sizes *Ecology Letters* 16:1446–1454.

Mucina, L. and Rutherford, M.C. 2006. The vegetation of South Africa, Lesotho and Swaziland. *Strelitzia* 19. South African National Biodiversity Institute, Pretoria Pg. 807–910.

Mucina, L., Rutherford, M.C., Palmer, A.R., Milton, S.J., Louis Scott, L., Lloyd, J.W., Merwe, B.V., Hoare, D.B., Bezuidenhout, H., Jan H.J. Vlok, J.H.J., Euston-Brown, D.I.W., Powrie, L.W. and Dold, A.P. 2006. Nama-Karoo Biome. *Strelitzia*, 9:328.

Münkemüller, T. Lavergne, S., Bzeznik, B., Dray, S., Jombart, T., Schiffers, K. and Thuiller, W. 2012. How to measure and test phylogenetic signal. *Methods in Ecology and Evolution* 3:743–756.

Münkemüller, T., Boucher, F.C., Thuiller, W. and Lavergne, S. 2015. Community phylogenetics and ecosystem functioning. Phylogenetic niche conservatism – common pitfalls and ways forward. *Functional Ecology* 29:627–639.

Murray, K.A., Rosauer, D., McCallum, H. and Skerratt, L.F. 2011. Integrating species traits with extrinsic threats: closing the gap between predicting and preventing species declines. *Proceedings of the Royal Society B: Biological Sciences* 278:1515–1523.

Musselman, L. J. and Haynes, S.C. 1996. Santalaceae with weed potential in the United States. pp 521–527 in M. T. Moreno, J. I. Cubero, D. Berner, D. Joel, L. J. Musselman, and C. Parker, eds. Advances in Parasitic Plant Research. Junta de Andalucia, Dirección General de Investigación Agraria, Cordoba, Spain.

Nasir, Y. 1984. Santalaceae. Pages 6. *Flora of Pakistan*. Pakistan Agricultural Research Council, Islamabad.

Nickrent, D.L. 2017. Status of the Genera *Colpoon, Osyris* and *Rhoiacarpos* in South Africa. *Bothalia*, 47(1):2260.

Nickrent, D.L. and García, M.A. 2015. *Lacomucinaea*, a new monotypic genus in Thesiaceae (Santalales). *Phytotaxa* 224(2):173–184.

Nickrent, D.L. and Musselman, L.J. 2004. Introduction to parasitic flowering plants. *The Plant Health Instructor*.

Nickrent, D.L., Malécot, V., Vidal-Russell, R. and Der, J.P. 2010. A revised classification of Santalales. *Taxon* 59(2):538–558.

Nixon, K.C. and Wheeler, Q.D. 1990. An amplification of the phylogenetic species concept. *Cladistics* 6:211–223.

Noguerales, V., Cordero, P.J.and Ortego, J. 2018. Integrating genomic and phenotypic data to

evaluate alternative phylogenetic and species delimitation hypotheses in a recent evolutionary radiation of grasshoppers. *Molecular Ecology* 27(5):1229–1244.

Noss, R.F., Platt, W.J., Sorrie, B.A., Weakley, A.S., Means, D.B., Costanza, J. and Peet, R.K. 2015. How global biodiversity hotspots may go unrecognized: lessons from the North American Coastal Plain. *Diversity and Distributions* 21:236–244.

Nuttal, T. 1818. The genera of North American plants and a catalogue of the species to the year 1817. Published by the author, Philadelphia.

Ohlemueller, R., Anderson, B.J. Araújo, M.B., Butchart, S.H.M., Kudrna, O., Ridgely, R.S. and Thomas, C.D. 2008. The coincidence of climatic and species rarity: high risk to small-range species from climate change. *Biology Letters* 4:568–572.

Pagel, M. 1999. Inferring the historical patterns of biological evolution. *Nature* 401:877–884

Pavoine S., Ollier S., Pontier D. and Chessel D. 2008. Testing for phylogenetic signal in phenotypic traits: new matrices of phylogenetic proximities. *Theoretical Population Biology* 73:79–91.

Pearson, R.G. and Dawson, T.P. 2003. Predicting the impact of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* 12: 361-371.

Pearson, R.G., Thuiller, W., Arau´jo, M.B., Martinez-Meyer, E., Brotons, L. and McClean, C. 2006. Model-based uncertainty in species range prediction. *Journal of Biogeography* 33:1704–1711.

Peltier, M. 2015. Plant Biodiversity of South-Western Morocco – Plante photographiée dans les environs de Midelt (Haut Atlas). Échirolles – France.

Perret, M., Chautems, A. and Spichiger, R. 2006. Dispersalvicariance analyses in the tribe Sinningieae (Gesneriaceae): a clue to understanding biogeographical history of the Brazilian Atlantic Forest. *Annals of the Missouri Botanical Garden* 93:340–358.

Peterson, A. Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M. and Araújo, M.B. 2012. Ecological niches and geographical distributions. Princeton, New Jersey: Princeton University Press. Pg. 315.

Phillips, S., Anderson, R.P., Dudík, M., Schapire, R., and Blair, M.E. 2017. Opening the black box: An open-source release of MaxEnt. *Ecography* 40:887–893.

Phillips, S.J., Anderson, R.P. and Schapire, R.E. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190:231–259.

Phytoimages, 2019. http://phytoimages.siu.edu/imgs/paraman1/r/Thesiaceae.Thesium.html. (Accessed on 8 January 2019).

Pilger, R. 1935. Santalaceae. In: Eckhardt, T. and Melchior, H. (Eds) *Die natürlichen Pflanzenfamilien*, Vol. 16b, 2nd Edn. W. Engelmann, Leipzig. Pg. 37–41.

Pio, D.V., Engler, R., Linder, P.L., Monadjem, A., Cotterill, F.P.D., Taylor, P.J., Schoeman, M., Price, B.W., Villet, M.H., Eick, G., Salamin, N. and Guisan, A. 2014. Climate change effects on animal and plant phylogenetic diversity in southern Africa. *Global Change Biology* 20:1538–1549.

Pirie, M.D. 2015. Phylogenies from concatenated data: Is the end nigh? *Taxon* 64:421–423.

Polatschek, A. 1982. Santalaceae in K. H. Rechinger, ed. Flora Iranica. Graz, Akademisch Druck.

Polhill, R.M. 2005. Santalaceae. Pages 1–22 in H. J. Beentje and S. A. Ghazanfar, eds. *Flora of Tropical East Africa*. Royal Botanic Gardens, Kew, Richmond.

Potts, A.J., Rebelo, T., Barrett, R.L. and Stirton, C.H. 2018. Hybridisation in the Cape and Kwongkan. *South African Journal of Botany* 118:282–283.

Pressey, R. L., Cabeza, M., Watts, M.E., Cowling, R.M. and Wilson, K.A. 2007. Conservation planning in a changing world. *Trends in Ecology and Evolution* 22:583.

Preuss, S., Low, M., Cassel-Lundhagen, A. and Berggren, A. 2014. Evaluating range-expansion models for calculating nonnative species' expansion rate. *Ecology and Evolution* 4(14):2812–2822.

Purvis, A., Gittleman, J.L., Cowlishaw, G. and Mace, G.M. 2000. Predicting extinction risk in declining species. *Proceedings of the Royal Society B: Biological Sciences* 267:1947–1952.

Qian, H. 2013. Environmental determinants of woody plant diversity at a regional scale in China. *PLoS ONE* 8:75–832.

R Core Team 2019. Integrated Development for R., Inc., Boston, MA.

Raimondo, D., Von Staden, L., Foden, W., Victor, J.E., Helme, N.A., Turner, R.C., Kamundi, D.A. and Manyama, P.A. 2009. Red List of South African Plants. *Strelitzia* 25. South African National Biodiversity Institute, Pretoria Pg. 668.

Rangel, T. F. and Loyola, R. D. 2012. Labelling ecological niche models. *Natureza & Conservação* 10(2):119–126.

Reichenbach, H.G. 1828. *Conspectus regni vegetabilis*. Lipsiae (Leipzig).

Rezende, V.L., Miranda, P.L.S., Meyer, L., Moreira, C.V., Linhares, M.F.M., Oliveira-Filho, A.T. and Eisenlohr, P.V. 2015. Tree species composition and richness along altitudinal gradients as a tool for conservation decisions: the case of Atlantic semideciduous forest. Biodiversity and Conservation, 24:2149–2163.

Ridley, M., 1993. Evolution. *Journal of Evolutionary Biology* 6:615–617.

Rodríguez-Castañeda, G., Hof, AR. Jansson, R. and Harding, L.E. 2012. Predicting the fate of biodiversity using species' distribution models: enhancing model comparability and repeatability. *PLoS ONE* 7:e44402.

Rogers, Z.S., Nickrent, D.L. and Malécot, V. 2008. *Staufferia* and *Pilgerina*: two new endemic monotypic arborescent genera of Santalaceae from Madagascar. *Annals of the Missouri Botanical Garden* 95:391–404.

Romo, A., Didukh, Y. and Boratynski, A. 2004. *Thesium* (Santalaceae) in Crimea, Ukraine. *Annals of Botany Fennici* 41:273–281.

Ronquist, F., Huelsenbeck, J.P. Larget, B., van der Mark, P., Simon, D. and Teslenko, M**.** 2017. MrBayes 3.2.6: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:1572–1574.

Sa'ad, F.M. 1983. Fam. 46: Santalaceae. *Flora of Egypt*. Cairo Academic Science Research and Technology. Pg 14–31.

Saiter, F.Z., Brown, J.L., Thomas, W.W., Oliveira-Filho, A.T and Carnaval, A.C. 2016. Environmental correlates of floristic regions and plant turnover in the Atlantic Forest hotspot. *Journal of Biogeography (J. Biogeogr.)* 43:2322–2331.

SANBI (South African Botanical Institute), 2015. Red List of South African Plants version 2017.1. http://redlist.sanbi.org/ (Accessed on 17 Aug 2018)

SANBI (South African National Biodiversity Institute) 2017. *Thesium* L. National Assessment: Red List of South African Plants version 2017.1. http://redlist.sanbi.org/ (Accessed on 2018/10/23).

Sandel, B., Monnet, A.C., Govaerts, R. and Vorontsova, M. 2017. Late Quaternary climate stability and the origins and future of global grass endemism. *Annals of Botany* 119:279–288.

Sassone, A.B., Giussani, L.M. and Guaglianone, E.R., 2013. Multivariate studies of Ipheion (Amaryllidaceae, Allioideae) and related genera. *Plant Systematics and Evolution* 229:1561–1575.

Savriama, Y. 2018. A Step-by-Step Guide for Geometric Morphometrics of Floral Symmetry. *Frontier of Plant Science* 9:1433.

Schmiedel, U. and Jürgens, N. 1999. Community structure on unusual habitat islands: quartz-fields in the Succulent Karoo, South Africa. *Plant Ecology* 142:57–69.

Schnitzler, J., Barraclough, T.G., Boatwright, J.S., Goldblatt, P., Manning, J.C., Powell, M.P., Rebelo, T. and Savolainen, V. 2011. Causes of Plant Diversification in the Cape

Biodiversity Hotspot of South Africa. *Systematic Biology* 60(3):343–357.

Schrire, B.D. and Lewis, G.P., 1996. Monophyly: a criterion for generic delimitation, with special reference to Leguminosae. In: van der Maesen L.J.G., van der Burgt X.M., van Medenbach de Rooy J.M. (eds) The Biodiversity of African Plants. Springer, Dordrecht. Pg. 353.

Schwartz, M.W., Iverson, L.R., Prasad, A.M., Matthews, S.N. and O'Connor, R.J. 2006. Predicting extinctions as a result of climate change. *Ecology* 87:1611–1615.

Sebola, R.J. and Balkwill, K., 2013. Calibration, verification and stepwise analysis for numerical phenetics: Olinia (Oliniaceae) as an example. *South African Journal of Botany* 88: 42–55.

Settele, J., Scholes, R., Betts, R., Bunn, S., Leadley, P. and Nepstad, D. 2014. Terrestrial and inland water systems. In: Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. (eds Field, C.B., Barros, V.R., Dokken, D.J., Mach, K.J., Mastrandrea, M.D., Bilir, T.E., Chatterjee, M., Ebi, K.L., Estrada, Y.O., Genova, R.C., Girma, B., Kissel, E.S., Levy, A.N., MacCracken, S., Mastrandrea, P.R. and White, L.L.). Cambridge University Press, Cambridge and New York, NY. Pg. 271–359.

Shaw, J., Lickey, E.B., Schilling, E.E. and Small, R.L. 2007. Comparison of whole chloroplast genome sequences to choose noncoding regions for phylogenetic studies in angiosperms: the tortoise and the hare III. *American Journal of Botany*. 94:275–288.

Shu, B.R.C. 2003. *Flora of China* 5:211–215.

Shutoh, K., Kaneko, S., Suetsugu, K., Naito, Y.I. and Kurosawa, T. 2016. Variation in vegetative morphology tracks the complex genetic diversification of the mycoheterotrophic species *Pyrola japonica* sensu lato. *American Journal of Botany* 103 (9):1618–1629.

Skeat, W.W. 1910. "Theism", in An Etymological Dictionary of the English Language, new edition, Oxford: The Clarendon Press, OCLC 582746570. Pg. 640.

Slatyer, C., Rosauer, D. and Lemckert, F. 2007. An assessment of endemism and species richness patterns in the Australian *Anura*. *Journal of Biogeography* 34:583-596.

Small, E. and Brookes, B., 1990. A taxonomic simplification of Medicago italica. *Canada Journal of Botany* 68: 2103–2111.

Sneath, P.H.A. 1976. Phenetic taxonomy at the species level and above. *Taxon* 25: 437 – 450.

Snijman, D.A. (ed.). 2013. *Plants of the Greater Cape Floristic Region, Vol. 2: The Extra Cape*

*flora*. Strelitzia 30. South African National Biodiversity Institute, Pretoria.

Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters* 10:1115–1123.

Soberón, J., Osorio-Olivera, L., and Peterson, T. 2017. Conceptual differences between ecological niche modeling and species distribution modeling. *Revista Mexicana de Biodiversidad* 88:437–441.

Sodhi, N.S., Bickford, D., Diesmos, A.C., Lee, T.M., Koh, L.P., Brook, B.W., Sekercioglu, C.H. and Bradshaw, C.J.A. 2008. Measuring the meltdown: drivers of global amphibian extinction and decline. *PLoS ONE* 3:e1636.

Sonder, W. 1857a. Enumeratio Santalacearum in Agrica australi extratropica crescentium. *Flora* 40(23):353–365.

Sonder, W. 1857b. Nachschrift zur meiner Enumeratio Santalacearum in Africa australi extratropica crescentium. *Flora* 40:401–407.

Soultan, A., Wikelski, M. and Safi, K. 2019. Risk of biodiversity collapse under climate change in the Afro-Arabian region. *Scientific Reports* 9:955.

Souza, S.M., Rodrigues, M.T. and Cohn-Haft, M. 2013. Are Amazonia rivers biogeographic barriers for lizards? A study on the geographic variation of the spectacled lizard Leposoma osvaldoi Avila-Pires (Squamata, Gymnophthalmidae). *Journal of Herpetology* 47:511–519.

Stace, C.A., 1989. Plant Taxonomy and Biosystematics. 2. ed. Edward Arnold, a division of Hodder and Stoughton, Cambridge, London.

Stearn, W.T., 1972. *Kunkeliella*, a New Genus of Santalaceae in the Canary Island. Cuad. Bat. Canar. XVP:11–26.

Sukumaran, J. and Knowles, L. 2017. Multispecies coalescent delimits structure, not species. *Proceedings of the National Academy of Sciences of the United States of America*. 114(7):1607–1612.

Swofford, D.L. 2016. PAUP: phylogenetic analysis using parsimony (and other methods) 4.0b10 Beta. Sinauer Associates. Sunderland, Massachusetts.

Taberlet, P., Gielly, L., Pautou, G. and Bouvet, J. 1991. Universal primers for amplification of three non-coding regions of chloroplast DNA. *Plant Molecular Biology* 17: 1105–1109.

The Angiosperm Phylogeny Group IV 2016. An update of the angiosperm phylogeny group classification for the orders and families of flowering plants: APG IV. *Journal of the Linnean Society* 181:1–20.

The Plant List, 2019. http://www.theplantlist.org/tpl1.1/search?q=Thesidium. (Accessed on 21 January 2019).

Thiers, B. 2019. [Continuously Updated] *Index Herbarium: a global directory of public herbaria and associated staff*. New York Botanical Garden, New York. http://sweetgum.nybg.org/science/ih/ (Accessed on 10/01/2019).

Thorn, J.S., Nijman, V., Smith, D. and Nekaris, K.A.I. 2009. Ecological niche modelling as a technique for assessing threats and setting conservation priorities for Asian slow lorises (Primates: *Nycticebus*). *Diversity and Distributions (Diversity Distrib.)* 15: 289–298.

Thuiller, W., Lavorel, S. and Araújo, M.B. 2005. Niche properties and geographical extent as predictors of species sensitivity to climate change. *Global Ecology and Biogeography* 14: 347–357.

Thuiller, W., Lavergne, S., Roquet, C., Boulangeat, I., Lafourcade, B. and Araújo, M.B. 2011. Consequences of climate change on the tree of life in Europe. *Nature* 470: 531–534.

Tibcom, 2018. http://www.tibco.com/Products/STATISTICA-Traits/Version-13. Accessed 28 August 2019.

Toledo, M., Pena-Claros, M., Bongers, F., Alarcon, A., Balc azar, J., Chuvina, J., Leano, C., Licona, J.C. and Poorter, L. 2012. Distribution patterns of tropical woody species in response to climatic and edaphic gradients. *Journal of Ecology* 100:253–263.

Topp, E.N. and Loos, J. 2019. Fragmented landscape, fragmented knowledge: a synthesis of Renosterveld ecology and conservation. *Environmental Conservation* 46:171–179.

Treurnicht, M., Colville, J.F., Joppa, L.N., Huyser, O. and Manning, J. 2017. Counting complete? Finalising the plant inventory of a global biodiversity hotspot. *Peer J* 5:e2984

Turland, N.J., Wiersema, J.H., Barrie, F.R. Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Kusber, W.-H., Li, D.-Z., Marhold, K., May, T.W., McNeill, J., Monro, A.M., Prado, J., Price, M.J. and Smith, G.F. 2018. *International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017*. Regnum Vegetabile 159. Koeltz Botanical Books, Glashütten.

Turvey, S.T. and Fritz, S.A. 2011. The ghosts of mammals' past: biological and geographical patterns of global mammalian extinction across the Holocene. *Philosophical Transactions of the Royal Society B* 366:2564–2576.

Urbina-Cardona, N., Blair, M.E., Londono, M.C., Loyola, R., Velasquez-Tibata, J., and Morales-Devia, H. 2019. Species distribution modeling in Latin America: A 25-Year retrospective review. *Tropical Conservation Science* 12:1–19.

Vamosi, J.C., Armbruster, W.S. and Renner, S.S. 2014. Evolutionary ecology of specialization: insights from phylogenetic analysis. *Proceedings of the Royal Society B: Biological*

*Sciences* 281:20142004.

Van der Loo, M. 2017. Package 'gower' version 0.1.2. http//github.com/markvanderloo/gower.

Van Proosdij, A.S.J., Sosef, M.S.M., Wieringa, J.J. and Raes, N. 2016. Minimum required number of specimen records to develop accurate species distribution models. *Ecography* 39:542–552.

Vazquez, D.P. and Simberloff, D. 2002. Ecological Specialization and Susceptibility to Disturbance: Conjectures and Refutations. *American Naturalist* 156(6):606–623.

Verboom, G.A., Linder, H.P., Forest, F., Hoffmann, V., Bergh, N.G. and Cowling, R.M. 2014. Cenozoic assembly of the Greater Cape flora in Fynbos: Ecology, Evolution, and Conservation of a Megadiverse Region. Oxford University Press. Pg. 93–118.

Verboom, G.A., Bergh, N.G., Haiden, S.A., Hoffmann, V. and Britton, M.N. 2015. Topography as a driver of diversification in the Cape Floristic Region of South Africa. *New Phytologist* 207:368–376.

Victor, J.E., Smith, G.F and van Wyk, A.E. 2016. History and drivers of plant taxonomy in South Africa. *Phytotaxa* 269(3):193–208.

Victor, J.E., Smith, G.F., and van Wyk, A.E. 2015. Strategy for plant taxonomic research in South Africa 2015–2020. SANBI Biodiversity Series 26. South African National Biodiversity Institute, Pretoria. Pp. 1–39.

Villero, D., Pla, M., Camps, D., Ruiz-Olmo, J., and Brotons, L. 2017. Integrating species distribution modelling into decision making to inform conservation actions. *Biodiversity and Conservation* 26:251–271.

Visser, N., Le Roux, M.M., and Ban Wyk, B.E. 2018. A taxonomic revision of the *Thesium goetzeanum* species complex (Santalaceae) from Lesotho, South Africa and Swaziland. *South African Journal of Botany* 119: 45–62. https://doi.org/10.1016/j.sajb.2018.08.005

Von Staden, L. 2015. *Thesium* L. National Assessment: Red List of South African Plants Version 2017.1. http://redlist.sanbi.org/ (Accessed on 2019/03/25).

Wang, Y., Fritsch, P.W. Shi, S., Almeda, F., Cruz, B.C. and Kelly, L.M. 2004. Phylogeny and infrageneric classification of Symplocos (Symplocaceae) inferred from DNA sequence data. *American Journal of Botany* 91(11):1901–1914.

Warren, D.L., Glor, R.E. and Turelli, M. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution* 62:2868–2883.

Weberling, F. 1989. Morphology of flowers and inflorescences. Cambridge University Press, Cambridge. Pg. 76.

White, T.J., Bruns, T., Lee, S. and Taylor, J. Ed. 1990. *Amplification and direct sequencing of*

*fungal ribosomal RNA genes for phylogenies*. Academic Press, San Diego.

Wickham, H. 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York. https://ggplot2.tidyverse.org.

Wiley, E.O. and Lieberman, B.S. 2011. Phylogenetics: Theory and Practice of Phylogenetic Systematics, 2nd Edi.

Williams, Y., Williams, S.E., Alford, R.A., Waycott, M. and Johnson, C.N. 2006. Niche breath and geographical range: ecological compensation for geographical rarity in rainforest frogs. *Biology Letters* 2:532–535.

Willis, C.G., Ruhfel, B.R., Primack, R.B., Miller-Rushing, A.J. and Losos, J.B. 2010. Favourable climate change response explains non-native species' success in Thoreau's Woods. *PLoS ONE* 5:e8878.

Willis, F., Moat, J. and Paton, A. 2003. Defining a role for herbarium data in Red List assessments: a case study of *Plectranthus* from eastern and southern tropical Africa. *Biodiversity and Conservation* 12:1537–1552.

Wisz, M.S., Hijmans, R.J., Li, J., Peterson, A.T., Graham, C.H., Guisan, A. 2008. Predicting Species Distributions Working Group. Effects of sample size on the performance of species distribution models. *Diversity and Distribution* 14:763-773.

Worldclim, 2019. https://www.worldclim.org/cmip5v1. Accessed 25/June/2019.

Van Wyk, V.A.E. and Smith, G.F. 2001. Regions of floristic endemism in southern Africa: a review with emphasis on succulents. Umdaus Press, Pretoria, South Africa. Pp 45

Yang, L. Hu, H. Xie, C. Lai, S. Yang, M. He, X. and Zhou, S. 2017. Molecular phylogeny, biogeography and ecological niche modelling of *Cardiocrinum* (Liliaceae): insights into the evolutionary history of endemic genera distributed across the Sino-Japanese floristic region. *Annals of Botany* 119 (1):59-72.

Yessoufou, K., Daru, B.H. and Davies, T.J. 2012. Phylogenetic Patterns of Extinction Risk in the Eastern Arc Ecosystems, an African Biodiversity Hotspot. *PLoS ONE* 7(10): e47082.

Yessoufou, K., Daru, B.H., Tafirei, R., Elansary, H.O. and Rampedi, I. 2016. Integrating biogeography, threat and evolutionary data to explore extinction crisis in the taxonomicgroup of cycads. *Ecology and Evolution* 7:2735–2746.

Zhang, C., Yang, J., Sha, L., Ci, X., Li, J., Cao, M., Brown, C., Swenson, N.G. and Lin, L. 2017. Lack of phylogenetic signals within environmental niches of tropical tree species across life stages. *Scientific Reports* 7:42007.

Zhigila, D.A., Verboom, G.A., Stirton, C.H. and Muasya, A.M. 2019a. A taxonomic revision of *Thesium* section *Hagnothesium* (Santalaceae) and description of a new species, *T.*

*quartzicolum. South African Journal of Botany* 124:280–303.

Zhigila, D.A., Verboom, G.A., Stirton, C.H., Smith, H. and Muasya, A.M. 2019b. Six new *Thesium* (Santalaceae) species endemic to the Greater Cape Floristic Region, South Africa, and one new name. *Phytotaxa* 423 (4):215–237.

Zhigila, D.A., Verboom, G.A. and Muasya, A.M. (accepted). An infrageneric classification of *Thesium* (Santalaceae) based on molecular phylogenetic data. *TAXON* 00 (00):1–24.

**Appendix Table S2.1:** Information on *Thesium* accessions used in this study. Accessions of four species in two genera, *Buckleya* and *Lacomucinaeae* were used as outgroups. The – represents missing sequences. GenBank numbers in bold indicate sequences generated for this study.

| | | GenBank number | | | |
|---|---|---|---|---|---|
| **Taxa** | **Voucher No.** | **ITS** | **trnL-F** | **MatK** | **rpl32-trnL** |
| *B.distichophylla* | – | – | EF464484.1 | DQ329191.1 | – |
| *B.lanceolata* | K 36067 | GU256863.1 | GU294669.1 | – | – |
| *L. lineata* | Nickrent 5509 | KP318960.1 | KP318970.1 | – | – |
| *L. lineata* | Nickrent 4800 | KP318959.1 | – | – | – |
| *L. lineata* | Nickrent 4726 | KP318958.1 | – | – | – |
| *L. lineata* | Nickrent 4725 | KP318957.1 | – | – | – |
| *L. lineata* | Nickrent 4413 | KP318956.1 | KP318969.1 | – | – |
| *T. acuminatum* | Moore149 | GU256845.1 | – | – | – |
| *T. acuminatum* | ZhigilaW1 | **MN242098** | **MN382910** | **MN382722** | **MN382761** |
| *T. acutissimum* | Muasya4944 | **MN242172** | **MN382842** | **MN382654** | **MN382757** |
| *T. acutissimum* | Muasya5159 | **MN242173** | **MN382947** | **MN382652** | **MN382756** |
| *T. aggregatum* | ABLouw12062 | GU256852.1 | GU294659.1 | – | – |
| *T. aggregatum* | Briton1904/085 | GU256836.1 | GU294649.1 | – | – |
| *T. aggregatum* | FForest694 | GU256832.1 | GU294646.1 | **MN382685** | – |
| *T. aggregatum* | FForest669 | GU256825.1 | – | – | – |
| *T. albomontanum* | Zhigila120 | **MN242109** | **MN382868** | – | – |
| *T. albomontanum* | Zhigila167 | **MN242111** | **MN382856** | – | – |
| *T. albomontanum* | Zhigila163 | **MN242205** | **MN382863** | **MN382855** | **MN382825** |
| *T. alpinum* | K36059 | GU256777.1 | GU294599.1 | – | – |
| *T. annulatum* | Zhigila142 | **MN242121** | – | – | – |
| *T. archeri* | Zhigila141 | **MN242101** | **MN382951** | **MN382851** | **MN382821** |
| *T. archeri* | Zhigila141b | **MN242149** | – | – | – |
| *T. aspermontanum* | Zhigila091 | **MN242113** | **MN382738** | **MN382736** | **MN382798** |
| *T. asterias* | TTS432 | GU256857.1 | GU294664.1 | – | – |
| *T. bathyschistum* | Moore87 1 | GU256847.1 | GU294654.1 | – | – |
| *T. bergeri* | K36060 | GU256778.1 | – | – | – |
| *T. brachygyne* | ABLouw11371 | GU256819.1 | GU294634.1 | – | – |
| *T. brachygyne* | Muasya7536 | – | **MN382858** | **MN382717** | **MN382802** |
| *T. brachygyne* | Muasya7535 | – | **MN382859** | **MN382719** | **MN382803** |
| *T. brasiliense* | K36058 | **GU294680.1** | – | – | – |
| *T. capitatum* | Moore111 | **GU256796.1** | – | – | – |
| *T. capitatum* | ZhigilaW2 | **MN242143** | – | **MN382657** | – |
| *T. capitatum* | Stirton14045 | **MN242188** | – | **MN382774** | – |
| *T. capitellatum* | ZhigilaW4 | **MN242161** | – | – | – |
| *T. capituliflorum* | Moore165 | GU256848.1 | GU294655.1 | – | – |
| *T. capituliflorum* | Muasya4083 | GU256844.1 | GU294652.1 | – | – |
| *T. capituliflorum* | Moore169 | GU256843.1 | | – | – |
| *T. capituliflorum* | Verboom1297 | GU256840.1 | GU294650.1 | – | – |

| | | | | | |
|---|---|---|---|---|---|
| *T. capituliflorum* | Muasya5586 | **MN242083** | **MN382934** | **MN382738** | – |
| *T. capituliflorum* | Zhigila159 | **MN242125** | **MN382867** | – | – |
| *T. carinatum* | Verboom1311 | GU256822.1 | GU294637.1 | – | – |
| *T. carinatum* | Moore167 | GU256798.1 | GU294618.1 | – | – |
| *T. carinatum* | FForest594 | GU256794.1 | – | – | – |
| *T. carinatum* | Zhigila101 | **MN242147** | **MN382873** | **MN382743** | **MN382768** |
| *T. carinatum* | Stirton14045 | – | **MN382926** | **MN382658** | – |
| *T. cf. angulosum* | Verboom 1025 | GU256854.1 | GU294661.1 | – | – |
| *T. cf. impeditum* | Verboom 1043 | GU256856.1 | GU294663.1 | – | – |
| *T. cf hillianum* | Zhigila165 | – | **MN382874** | **MN382686** | **MN382823** |
| *T. cf impeditum* | Zhigila157 | – | **MN382941** | – | – |
| *T. cf transluscens* | Zhigila090 | – | **MN382886** | **MN382680** | **MN382840** |
| *T. chinense* | K36065 | GU256781.1 | GU294603.1 | – | – |
| *T. chinense* | K36063 | – | GU294673.1 | – | – |
| *T. cilicicum* | Nickrent 4838 | KP318965.1 | – | – | – |
| *T. commutatum* | Zhigila076 | **MN242134** | **MN382850** | **MN382712** | **MN382775** |
| *T. commutatum* | Zhigila095 | – | **MN382851** | **MN382733** | **MN382769** |
| *T. commutatum* | Zhigila094 | – | **MN382875** | **MN382734** | – |
| *T. cornigerum* | FForest952 | GU256833.1 | GU294647.1 | – | – |
| *T. corymbeligerum* | Helme1604 | **MN242180** | **MN382936** | **MN382661** | **MN382826** |
| *T. costatum* | Verboom1037 | GU256855.1 | GU294662.1 | – | – |
| *T. crassifolium* | Zhigila140 | **MN242150** | – | – | – |
| *T. cupressoides* | Verboom1026 | GU256859.1 | GU294666.1 | – | – |
| *T. cuspidatum* | Muasya4026 | **MN242164** | **MN382931** | **MN382689** | – |
| *T. densiflorum* | Moore 152 | – | GU294679.1 | – | – |
| *T. densiflorum* | Stirton13384 | – | **MN382911** | **MN382718** | – |
| *T. dinteri* | Helme5505 | **MN242166** | **MN382917** | **MN382694** | **MN382834** |
| *T. dinteri* | Stirton13774 | **MN382716** | **MN382915** | **MN382711** | **MN382788** |
| *T. dissitifolium* | Zhigila136 | **MN242177** | **MN382864** | **MN382751** | **MN382831** |
| *T. diversifolium* | Zhigila080 | **MN242140** | **MN382892** | **MN382656** | **MN382793** |
| *T. diversifolium* | Zhigila082 | **MN242145** | **MN382893** | **MN382676** | **MN382790** |
| *T. dmmagiae* | Zhigila156 | **MN242192** | **MN382925** | **MN382749** | **MN382816** |
| *T. ecklonianum* | Zhigila271 | **MN242148** | **MN382935** | **MN382740** | **MN382764** |
| *T. elatius* | Helme7588 | **MN242156** | **MN382866** | **MN382704** | **MN382781** |
| *T. ericaefolium* | Zhigila155 | **MN242104** | **MN382855** | **MN382682** | – |
| *T. ericaefolium2* | Zhigila158 | **MN242105** | **MN382852** | – | – |
| *T. ericafolium* | Zhigila255 | **MN242106** | **MN382967** | – | **MN382820** |
| *T. ericifolium* | Verboom1296 | GU256816.1 | GU294631.1 | – | – |
| *T. ericifolium* | Moore89 | GU256803.1 | GU294623.1 | KP110164.1 | – |
| *T. euphorbioides* | FForest953 | GU256791.1 | GU294614.1 | KP110165.1 | – |
| *T. euphrasioides* | Zhigila078 | – | **MN382860** | **MN382684** | **MN382839** |
| *T. euphrasioides* | Striton13781 | **MN242165** | **MN382897** | **MN382725** | **MN382835** |
| *T. fallax* | Zhigila117 | **MN242196** | **Zhigila097** | **MN382754** | **MN382787** |
| *T. flexuosum* | Verboom1156 | GU256815.1 | GU294630.1 | **MN382745** | – |
| *T. flexuosum* | Muasya5046 | **MN242182** | **MN382888** | **MN382687** | **MN382809** |
| *T. foliosum* | Moore41 | GU256799.1 | GU294619.1 | – | – |

| | | | | | |
|---|---|---|---|---|---|
| *T. fragile* | Verboom912 | GU256783.1 | GU294606.1 | – | – |
| *T. fragile* | Verboom1305 | – | GU294681.1 | – | – |
| *T. fragile* | Zhigila106 | **MN242204** | **MN382938** | **MN382753** | **MN382837** |
| *T. frisea* | AB LouwWV14 | – | GU294678.1 | – | – |
| *T. frisea* | FForestCP3 | GU256826.1 | GU294640.1 | – | – |
| *T. frisea* | NGBergh1616 | GU256809.1 | GU294626.1 | – | – |
| *T. frisea* | Zhigila254 | **MN242123** | **MN382921** | – | **MN382801** |
| *T. frisea* | Zhigila266 | **MN242124** | **MN382877** | – | **MN382822** |
| *T. fruticosum* | Nickrent 4115 | – | – | EF584633.1 | – |
| *T. fruticosum* | Zhigila112 | **MN242110** | **MN382901** | **MN382703** | **MN382776** |
| *T. fruticulosum* | Zhigila114 | **MN242206** | **Zhigila098** | **MN382721** | – |
| *T. funale* | Zhigila115 | **MN242137** | **MN382899** | **MN382700** | **MN382789** |
| *T. funale* | FForest732 | GU256866.1 | – | – | – |
| *T. funale* | Zhigila020 | **MN242115** | **MN382909** | **MN382696** | **MN382829** |
| *T. funale* | Zhigila038 | **MN242119** | **MN382882** | **MN382655** | – |
| *T. galioides* | Moore50 | GU256792.1 | GU294615.1 | – | – |
| *T. galioides* | Zhigila129 | **MN242200** | **MN382961** | – | – |
| *T. glomeratum* | Zhigila138 | **MN242153** | **MN382946** | – | – |
| *T. glomeruliflorum* | Moore46 | GU256801.1 | GU294621.1 | – | – |
| *T. glomeruliflorum* | Muasya4767 | **MN242112** | **MN382965** | **MN382705** | **MN382807** |
| *T. gnidiaceum* | Zhigila118 | **MN242179** | **MN382883** | – | – |
| *T. gracile* | TLNowellsn | GU256862.1 | GU294668.1 | – | – |
| *T. gracile* | Verboom1054b | GU256861.1 | – | – | – |
| *T. gracile* | Verboom1054a | GU256860.1 | GU294667.1 | – | – |
| *T. gracile* | TTS424 | GU256858.1 | GU294665.1 | – | – |
| *T. helichrysioides* | Zhigila121 | **MN242195** | **MN382923** | **MN382701** | **MN382767** |
| *T. hispidulum* | ABLouw9440 | GU256820.1 | GU294635.1 | – | – |
| *T. hispidulum* | Stirton13493 | – | **MN382872** | – | – |
| *T. hollandii* | Zhigila125 | **MN242176** | **MN382964** | – | **MN382778** |
| *T. humifusum* | Chase1881 | GU256780.1 | GU294602.1 | – | – |
| *T. humifusum* | NMW980 | KX167150.1 | GU294604.1 | JN894197.1 | – |
| *T. humifusum* | NMW4593 | KX166656.1 | – | JN895002.1 | – |
| *T. humifusum* | MIB:ZPL:03211 | – | – | HE967500.1 | – |
| *T. humile* | MMGhanisn | – | GU294674.1 | – | – |
| *T. hystricoides* | Britain4642 | **MN242178** | – | – | **MN382832** |
| *T. hystrix* | Stirton13426 | **MN242168** | **MN382928** | **MN382750** | – |
| *T. imbricatum* | TTS423 | GU256810.1 | – | – | – |
| *T. impeditum* | – | AF291908.1 | – | EF584634.1 | – |
| *T. impeditum* | Zhigila157 | MN242189 | – | – | – |
| *T. impressum* | K 36056 | GU256776.1 | GU294598.1 | – | – |
| *T. juncifolium* | Moore62 | GU256846.1 | GU294653.1 | – | – |
| *T. juncifolium* | Moore54 | – | GU294675.1 | – | – |
| *T. juncifolium* | Muasya4081 | GU256834.1 | – | – | – |
| *T. karooicum* | Zhigila160 | **MN242181** | **MN382948** | **MN382708** | **MN382815** |
| *T. lacinulatum* | Zhigila135 | – | **MN382957** | – | – |
| *T. lisae-mariae* | Zhigila105 | – | **MN382857** | **MN382713** | **MN382786** |

| | | | | | |
|---|---|---|---|---|---|
| *T. leptocaule* | FForest768 | GU256804.1 | GU294624.1 | – | – |
| *T. leptostachyum* | FForest1 | GU256784.1 | GU294607.1 | – | – |
| *T. linophyllon* | XT34 | – | – | KJ746196.1 | – |
| *T. litoreum* | Stirton13464 | **MN242117** | **MN382881** | **MN382771** | **MN382771** |
| *T. lopollense* | Angola1959 | GU256823.1 | GU294638.1 | – | – |
| *T. macrostachyum* | Moore168 | GU256850.1 | GU294657.1 | – | – |
| *T. macrostachyum* | Moore166 | GU256849.1 | GU294656.1 | – | – |
| *T. macrostachyum* | Moore140 | GU256839.1 | – | – | – |
| *T. mauritanicum* | Nickrent 5193 | KP318967.1 | – | – | – |
| *T. mauritanicum* | Nickrent 4844 | KP318966.1 | – | – | – |
| *T. microcarpum* | Verboom1150 | GU256786.1 | GU294609.1 | – | – |
| *T. microcarpum* | | – | – | KP110162.1 | – |
| *T. microcarpum* | Verboom1149 | GU256785.1 | GU294608.1 | – | – |
| *T. microcarpum* | Zhigila149 | **MN242201** | **MN382940** | – | – |
| *T. microcarpum* | Zhigila150 | **MN242202** | **MN382941** | **MN382744** | **MN382836** |
| *T. micromeria* | Zhigila113 | **MN242116** | **MN382862** | **MN382715** | – |
| *T. micromeria* | Muasya7536 | **MN242136** | – | – | **MN382782** |
| *T. micropogon* | Zhigila029 | **MN242132** | **MN382895** | **MN382673** | **MN382792** |
| *T. minkwitzianum* | Nickrent 5112 | KP318964.1 | – | – | – |
| *T. minus* | Zhigila116 | MN242207 | MN382954 | MN382710 | – |
| *T. namaquense* | FForest896 | GU256789.1 | GU294612.1 | – | – |
| *T. namaquense* | Zhigila168 | **MN242102** | – | – | – |
| *T. neoprostratum* | Zhigila081 | **MN242082** | **MN382920** | **MN382668** | **MN382772** |
| *T. neoprostratum* | Zhigila086a | **MN242133** | **MN382919** | – | **MN382799** |
| *T. nigromontanum* | FForest702 | GU256829.1 | GU294643.1 | – | – |
| *T. nigromontanum* | Zhigila162 | **MN242091** | **MN382908** | **MN382706** | – |
| *T. nigromontanum* | Muasya5559 | **MN242151** | **MN382960** | **MN382735** | **MN382827** |
| *T. nigroperianthum* | Zhigila151 | **MN242090** | **MN382956** | **MN382741** | **MN382824** |
| *T. nigroperianthum* | Zhigila283 | **MN242127** | **MN382957** | – | – |
| *T. nudicaule* | ABLouw12249 | GU256818.1 | GU294633.1 | – | – |
| *T. nudicaule* | Zhigila131 | **MN242193** | **MN382878** | **MN382691** | – |
| *T. nudicaule* | Zhigila088 | – | **MN382913** | **MN382663** | **MN382761** |
| *T. occidentale* | Muasya4780 | – | – | **MN382675** | **MN382761** |
| *T. orientale* | Zhigila143 | – | – | **MN382671** | – |
| *T. paniculatum* | Moore23 | GU256821.1 | GU294636.1 | – | – |
| *T. paniculatum* | Zhigila100 | **MN242191** | **MN382905** | **MN382726** | **MN382838** |
| *T. paronychioides* | Zhigila130 | **MN242103** | **MN382933** | – | – |
| *T. paronychoides* | Zhigila122 | **MN242194** | – | – | – |
| *T. patulum* | DGEvans25 | GU256827.1 | GU294641.1 | – | – |
| *T. penicillatum* | Verboom1140 | GU256814.1 | GU294629.1 | – | – |
| *T. pinifolium* | Moore43 | GU256800.1 | GU294620.1 | – | – |
| *T. polycephalum* | Verboom1142 | GU256842.1 | GU294651.1 | – | – |
| *T. polycephalum* | FForest911 | GU256790.1 | GU294613.1 | – | – |
| *T. procumbens* | K36061 | – | GU294672.1 | – | – |
| *T. prostratum* | Zhigila086b | **MN242129** | **MN382890** | **MN382697** | – |
| *T. prostratum* | Zhigila089 | **MN242146** | **MN382891** | **MN382688** | – |

| | | | | | |
|---|---|---|---|---|---|
| *T. pseudovirgatum* | Briton1904/084 | GU256835.1 | GU294648.1 | – | **MN382762** |
| *T. pseudovirgatum* | Zhigila096 | **MN382902** | **MN382876** | **MN382707** | **MN382806** |
| *T. pseudovirgatum* | Zhigila034 | – | – | **MN382683** | **MN382762** |
| *T. pubescens* | F Forest CP4 | – | GU294682.1 | – | – |
| *T. pubescens* | Zhigila133 | **MN242096** | **MN382949** | – | **MN382817** |
| *T. pubescens* | Stirton13746 | **MN242167** | **MN382943** | **MN382755** | **MN382773** |
| *T. pubescens* | Muasya4798 | **MN242169** | **MN382942** | **MN382669** | **MN382773** |
| *T. pungens* | Verboom1340 | GU256812.1 | GU294628.1 | – | – |
| *T. pycnanthum* | Britton1904/082 | GU256797.1 | GU294617.1 | – | – |
| *T. pycnanthum* | Muasya4301 | – | – | **MN382752** | **MN382784** |
| *T. quartzicolum* | Zhigila026 | **MN242203** | **MN382939** | **MN382747** | **MN382791** |
| *T. quinqueflorum* | Muasya4238 | **MN242084** | **MN382887** | **MN382739** | **MN382796** |
| *T. racemosum* | Zhigila128 | **MN382709** | **MN382844** | – | – |
| *T. radicans* | K36062 | GU256779.1 | GU294601.1 | – | – |
| *T. rariflorum* | Moore100 | GU256841.1 | – | – | – |
| *T. retamoides* | Nickrent 5559 | KP318961.1 | – | – | – |
| *T. rhizomatum* | Zhigila153 | **MN242089** | **MN382918** | **MN382693** | – |
| *T. rhizomatum* | Zhigila280 | **MN242197** | **MN382944** | **MN382694** | – |
| *T. rhizomatum* | Zhigila152 | **MN242198** | **MN382918** | **MN382716** | **MN382800** |
| *T. rufescens* | Stirton14093 | – | – | **MN382660** | **MN382765** |
| *T. sawae* | Zhigila075 | **MN242092** | **MN382927** | **MN382678** | **MN382766** |
| *T. sawae* | Zhigila079 | **MN242144** | **MN382930** | **MN382659** | **MN382770** |
| *T. scabrum* | Moore155 | **GU256808.1** | – | – | – |
| *T. scabrum* | Muasya4121 | **MN242184** | **MN382955** | **MN382667** | – |
| *T. scabrum* | Stirton13369 | **MN242185** | **MN382924** | **MN382666** | **MN382841** |
| *T. scandens* | Zhigila134 | **MN242155** | **MN382845** | – | – |
| *T. schumannianum* | Zhigila269 | **MN242087** | **MN382953** | – | **MN382813** |
| *T. schweinfurthii* | K36066 | GU256782.1 | GU294605.1 | – | – |
| *T. scirpioides* | Muasya5515 | – | **MN382943** | **MN382679** | – |
| *T. selagineum* | Stirton14151 | – | **MN382907** | **MN382756** | **MN382830** |
| *T. sonderianum* | Zhigila122 | – | **MN382929** | – | – |
| *T. sedifolium* | Moore146 | GU256807.1 | – | – | – |
| *T. sertulariastrum* | Moore 45 | – | GU294676.1 | – | – |
| *T. sp* | Zhigila096 | **MN242114** | – | – | – |
| *T. sp* | Zhigila078 | **MN242118** | – | – | – |
| *T. sp* | Muasya5562 | **MN242120** | **MN382932** | – | – |
| *T. sp* | Zhigila022 | **MN242122** | **MN382870** | – | – |
| *T. sp* | Zhigila023 | **MN242126** | **MN382871** | – | – |
| *T. sp* | Muasya4780 | **MN242128** | **MN382950** | – | – |
| *T. sp* | Zhigila077 | **MN242130** | **MN382861** | **MN382714** | |
| *T. sp* | Stirton13493 | **MN242135** | – | – | – |
| *T. sp* | Zhigila092 | **MN242138** | **MN382925** | – | – |
| *T. sp* | Muasya7535 | **MN242139** | – | **MN382695** | – |
| *T. sp* | Stirton14093 | **MN242142** | **MN382912** | **MN382671** | – |
| *T. sp* | Muasya5515 | **MN242152** | – | – | – |
| *T. sp* | Stirton13648 | **MN242154** | – | **MN382670** | **MN382763** |

| | | | | | |
|---|---|---|---|---|---|
| *T. sp* | Zhigila097 | **MN242158** | **MN382848** | – | **MN382783** |
| *T. sp* | Zhigila087 | **MN242160** | **MN382889** | – | **MN382759** |
| *T. sp* | Zhigila099 | **MN242162** | **MN382904** | – | **MN382795** |
| *T. sp* | Zhigila079 | **MN242163** | – | – | – |
| *T. sp* | Zhigila165 | **MN242170** | – | – | – |
| *T. sp* | Zhigila164 | **MN242199** | **MN382885** | **MN382681** | **MN382818** |
| *T. sp. TEM-2009* | Verboom1290 | GU256851.1 | GU294658.1 | – | – |
| *T. sp. TEM-2009* | Moore16 | GU256831.1 | GU294645.1 | – | – |
| *T. sp1* | Zhigila090 | **MN242085** | – | – | – |
| T. sp2 | Zhigila095 | **MN242086** | **MN382903** | – | – |
| *T. sp3* | Muasya4083 | **MN242088** | **MN382903** | – | – |
| *T. sp4* | Stirton13324 | **MN242093** | – | – | **MN382794** |
| *T. sp5* | Zhigila098 | **MN242095** | **MN382890** | – | **MN382795** |
| *T. sp6* | Muasya4733 | **MN242099** | **MN382944** | – | **MN382758** |
| *T. sp7* | Zhigila084 | **MN242100** | – | – | – |
| *T. spicatum* | Verboom1300 | GU256853.1 | GU294660.1 | – | – |
| *T. spicatum* | FForest850 | GU256830.1 | GU294644.1 | – | – |
| *T. spicatum* | FForest950 | GU256828.1 | GU294642.1 | – | – |
| *T. spicatum* | Zhigila147 | **MN242131** | **MN382963** | – | – |
| *T. spicatum* | Muasya5550 | – | – | **MN382737** | – |
| *T. spicatum* | Zhigila146 | **MN242171** | – | – | – |
| *T. spinosum* | Moore114 | GU256805.1 | – | – | – |
| *T. spinulosum* | Moore148 | GU256811.1 | GU294627.1 | – | – |
| *T. squarrosum* | FForest851 | GU256787.1 | GU294610.1 | – | – |
| *T. squarrosum* | Zhigila123 | **MN242174** | **MN382959** | – | – |
| *T. stelleroides* | Nickrent4848 | KP318963.1 | – | – | – |
| *T. stirtonii* | Zhigila021 | **MN242183** | **MN382885** | **MN382724** | **MN382797** |
| *T. stirtonii* | Muasya7540 | **MN242186** | **MN382883** | **MN382662** | **MN382811** |
| *T. stirtonii* | Zhigila148 | **MN242187** | **MN382884** | – | – |
| *T. strictum* | Zhigila264 | **MN242108** | **MN382922** | – | **MN382814** |
| *T. strictum* | FForest668 | GU256813.1 | – | – | – |
| *T. strictum* | Verboom 1295 | – | GU294677.1 | – | – |
| *T. strictum* | Moore48 | GU256802.1 | GU294622.1 | – | – |
| *T. strictum* | Zhigila256 | **MN242107** | **MN382952** | – | **MN382819** |
| *T. subnudum* | Moore96 | GU256837.1 | – | **MN382728** | – |
| *T. subnudum* | ABLouw9563 | GU256817.1 | GU294632.1 | – | – |
| *T. subnudum* | Muasya4042 | **MN242141** | **MN382945** | – | – |
| *T. subsucculentum* | Nickrent4374 | KP318962.1 | – | – | – |
| *T. subsucculenta* | Guerra S.N4374 | – | – | EF584621.1 | |
| *T. susannae* | Zhigila127 | **MN242097** | **MN382898** | – | – |
| *T. tepuiense* | K36057 | GU256824.1 | GU294639.1 | – | – |
| *T. translucens* | Britton1904 | GU256795.1 | – | – | – |
| *T. transvaalense* | Burrows1153 | **MN242175** | **MN382843** | **MN382653** | **MN382833** |
| *T. triflorum* | Moore128 | GU256788.1 | GU294611.1 | – | – |
| *T. triflorum* | Zhigila137 | – | **MN382846** | – | – |
| *T. urceolatum* | Zhigila119 | **MN242157** | **MN382847** | – | – |

| | | | | | |
|---|---|---|---|---|---|
| *T. virgatum* | Moore14 | GU256838.1 | – | – | – |
| *T. virgatum* | Verboom1153 | GU256806.1 | GU294625.1 | – | – |
| *T. virgatum* | Zhigila102 | **MN242159** | **MN382853** | **MN382727** | **MN382808** |
| *T. virgatum* | – | – | – | KP110166.1 | – |
| *T. viridifolium* | FForest680 | GU256793.1 | GU294616.1 | – | – |
| *T. viridifolium* | ZhigilaW3 | **MN242094** | **MN382962** | **MN382690** | **MN382760** |
| *T. whitehillensis* | Zhigila161 | **MN242190** | **MN382865** | **MN382742** | **MN382812** |

**Appendix Table S2.2:** Coded data matrix for morphological data.

The following format is used: Taxa, Habit, Plant Height (cm), Rootstock, Aerial stem, Stem Surface, Plant scabrid, Branching pattern, Stem brittle, Leaf length (mm), Leafiness, Leaf shape, Leaf attachment, leaves succulent, Leaf apex, Leaf margin, Leaf margin texture,Leaf midrib, Flower, Inflorescence Type, Flower shape, Peduncle, Flower bract length, Flower bract shape, Flower Bract margin texture, Flower Bract margin aspect, Flower bract apex, Flower bract midrib, Bracteole, Flower merosity, Hypanthial tube aspect, Stigma anther relationship, Floral trichome, Corolla lobe shape, Corolla lobe tip, Corolla lobulate, Apical papillae, Corolla lobe margin, Corolla lobe inside colour, Corolla lobe outside colour, Fruit, Fruit surface, Fruit shape, Fruit elaiosome, Fruit rib, Fruit colour, Fruit length (mm), Fruit width (mm), Length of persistent perianth

acutMM4944,0,2,1,0,0,0,0,0,3,1,0,0,0,1,0,0,1,1,0,0,1,0,0,0,1,0,0,1,0,1,0,0,1,0,1,0,0,0,1,0,0,0,0,0,0,1,1

acutMM5159,0,2,1,0,0,0,0,0,3,1,0,0,0,1,0,0,1,1,0,0,1,0,0,0,1,0,0,1,0,1,0,0,1,0,1,0,0,0,1,0,0,0,0,0,0,1,1

aggAB12062,1,4,0,0,1,0,0,0,3,0,0,0,1,0,0,0,0,0,1,0,1,0,1,0,0,1,0,1,1,0,1,0,1,1,0,0,1,0,0,0,0,1,0,0,0,0,0,0

aggreFF694,1,4,0,0,1,0,0,0,3,0,0,0,1,0,0,0,0,0,1,0,1,0,1,0,0,1,0,1,1,0,1,0,1,1,0,0,1,0,0,0,0,1,0,0,0,0,0,0,

aggregZ020,1,4,0,0,1,0,0,0,3,0,0,0,1,0,0,0,0,0,1,0,1,0,1,0,0,1,0,1,1,0,1,0,1,1,0,0,1,0,0,0,0,1,0,0,0,0,0,0,0

aggretZ266,1,4,0,0,1,0,0,0,3,0,0,0,1,0,0,0,0,0,1,0,1,0,1,0,0,1,0,1,1,0,1,0,1,1,0,0,1,0,0,0,0,1,0,0,0,0,0,0,0

alatMM7534,1,2,0,1,0,0,1,0,2,1,2,0,1,0,0,0,0,0,1,0,1,0,1,0,0,0,0,0,0,1,0,?,0,1,1,0,1,1,0,0,2,0,0,0,0,2,2,?,?,2

albomoZ120,0,2,0,0,1,0,0,0,0,0,1,2,0,1,0,0,0,0,0,1,0,0,0,0,1,1,0,0,0,0,0,1,0,?,0,0,0,0,1,1,0,0,0,0,1,0,0,0,0,0,0,?,?,1

albomoZ163,0,2,0,0,1,0,0,0,0,0,1,2,0,1,0,0,0,0,0,1,0,0,0,0,1,1,0,0,0,0,0,1,6,?,0,0,0,0,1,1,0,0,0,0,1,0,0,0,0,0,0,?,?,1

alpiK36059,0,?,1,1,0,0,1,0,?,1,0,1,0,0,0,0,0,0,1,0,0,1,0,0,0,0,0,0,0,1,0,1,1,0,0,0,0,1,0,1,0,1,0,0,0,1,0,1,?,?,0

angulV1025,0,4,0,0,0,0,0,0,0,0,1,0,0,0,0,0,1,1,1,1,3,0,1,1,0,1,1,0,0,1,0,1,0,0,0,0,1,0,1,2,?,?,0,0,1,1,0,0,1,1,0

annulaZ142,1,0,?,0,0,0,1,0,2,1,0,0,1,0,0,?,1,1,0,?,?,2,0,0,0,0,0,1,1,0,?,?,1,0,?,?,1,?,0,1,0,?,?,?,?,?,?,?,?

archerZ141,0,4,0,0,0,?,0,0,?,?,?,0,?,?,?,?,?,1,?,?,?,?,?,?,?,?,?,?,?,?,?,?,0,?,?,?,?,?,?,?,?,0,0,0,?,?,0,1,1,?

arvenseF05,2,2,0,0,1,1,1,?,4,0,2,2,0,0,1,0,0,1,4,1,1,0,0,0,1,0,0,1,2,1,1,0,0,0,0,1,1,0,1,0,1,0,0,1,1,1,0,0

arvenseG05,2,2,0,0,1,1,1,?,4,0,2,2,0,0,1,0,0,1,4,1,1,0,0,0,1,0,0,1,2,1,1,0,0,0,0,1,1,0,1,0,1,0,0,1,1,1,0,0,0,0

asteTTS432,0,2,1,0,0,?,0,0,?,?,0,0,?,1,0,0,0,1,4,0,0,0,1,0,1,0,0,1,0,?,0,0,0,?,?,0,0,0,?,0,0,0,?,0,0,0,0,0,?

bathystM87,1,2,0,0,0,0,0,0,0,1,1,3,0,1,0,?,?,?,1,0,1,?,0,0,?,0,0,0,0,1,0,1,?,1,2,1,0,1,2,0,1,0,1,2,?,0,0,1,1

Bdisticho,0,2,?,?,?,?,?,0,?,?,?,?,?,?,?,?,?,?,1,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,0,?,?,?,?,?,?,?,?

bergK36060,0,?,0,0,1,1,0,0,?,1,0,1,0,0,1,1,0,1,0,2,1,0,0,0,1,0,0,1,0,1,1,0,0,0,0,0,1,0,1,0,1,0,1,0,1,?,

BlaK36067,?,?,?,?,?,?,?,?,0,?,?,?,?,?,?,?,?,?,?,1,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,0,?,?,?,?,?,?,?,?

braAB11371,0,2,1,1,0,0,0,0,1,0,2,0,0,1,0,1,1,1,0,0,1,0,0,0,1,0,0,1,0,1,0,1,1,1,0,1,0,0,1,0,1,0,0,0,0,0

brasK36058,?,?,1,?,0,0,?,0,?,0,?,?,?,?,?,?,?,?,1,4,1,1,1,1,0,1,0,0,?,0,1,?,?,?,?,0,?,?,0,1,0,1,0,0,0,0,0,0,0
capfloM165,1,1,1,1,0,0,2,0,1,2,2,0,1,0,0,0,0,0,1,3,1,0,1,0,0,0,1,0,1,0,?,0,1,1,0,1,1,0,0,1,0,0,0,0,0,0,?,?,1
capflV1297,1,1,1,1,0,0,2,0,1,2,2,0,1,0,0,0,0,0,1,3,1,0,1,0,0,0,1,0,1,0,?,0,1,1,0,1,1,0,0,1,0,0,0,0,0,0,?,?,1
capfMS4083,1,1,1,1,0,0,2,0,1,2,2,0,1,0,0,0,0,0,1,3,1,0,1,0,0,0,1,0,1,0,?,0,1,1,0,1,1,0,0,1,0,0,0,0,0,0,?,?,1
capitatuW1,0,2,0,0,1,0,0,0,?,1,0,0,1,0,0,0,1,1,3,1,0,0,0,1,1,0,1,1,0,?,0,1,1,0,0,1,2,0,1,0,0,0,0,0,0,?,?,0
carinaM167,0,2,0,0,1,0,0,0,2,1,0,0,1,0,0,1,1,1,3,1,0,0,0,1,1,0,1,1,0,?,0,1,1,0,0,1,2,0,1,0,1,0,0,0,0,0,0,0
carinaZ101,0,2,0,0,1,0,0,0,2,1,0,0,1,0,0,1,1,1,3,1,0,0,0,1,1,0,1,1,0,?,0,1,1,0,0,1,2,0,1,0,1,0,0,0,0,0,0,0
carinV1311,0,2,0,0,1,0,0,0,2,1,0,0,1,0,0,1,1,1,3,1,0,0,0,1,1,0,1,1,0,?,0,1,1,0,0,1,2,0,1,0,1,0,0,0,0,0,0,0
carpldZ035,1,1,1,1,1,0,0,0,2,1,0,0,1,0,0,0,1,1,3,1,1,0,0,1,1,0,1,1,0,?,0,1,1,0,0,1,2,0,1,0,1,0,0,0,0,0,0,0
carpldZ075,1,1,1,1,1,0,0,0,2,1,0,0,1,0,0,0,1,1,3,1,1,0,0,1,1,0,1,1,0,?,0,1,1,0,0,1,2,0,1,0,1,0,0,0,0,0,0,0
chinK36063,2,?,1,0,0,0,0,0,?,1,0,1,0,0,0,0,0,0,1,4,1,1,0,0,0,1,0,1,1,3,1,1,0,1,1,0,0,2,0,1,0,0,0,1,0,1,?,?,0
chinK36065,2,?,1,0,0,0,0,0,?,1,0,1,0,0,0,0,0,0,1,4,1,1,0,0,0,1,0,1,1,3,1,1,0,1,1,0,0,2,0,1,0,0,0,1,0,1,?,?,0
cilicN4838,2,0,1,0,1,0,0,0,3,1,0,0,0,0,0,0,0,0,1,4,1,1,0,0,0,1,0,0,1,0,1,?,1,2,1,0,1,0,0,1,0,0,0,?,0,0,?,?,0
corniFF952,2,?,1,0,1,0,0,0,2,0,0,0,0,0,0,0,?,1,1,4,1,1,1,0,?,?,0,?,?,0,?,?,1,1,1,?,1,0,0,1,0,?,?,?,?,?,?,?,?
corymH1604,0,2,1,0,0,0,0,0,0,2,0,0,0,0,0,0,0,0,1,1,0,1,1,1,0,1,0,0,1,0,1,0,0,0,1,1,1,2,?,?,0,?,?,?,?,?,1,1,?
costaV1037,0,?,1,0,1,0,0,0,3,1,0,0,0,1,0,0,1,1,3,0,1,2,0,0,1,0,0,1,0,?,0,0,0,1,1,1,2,?,?,0,1,0,?,0,?,?,?,?
crassiZ140,1,2,0,0,1,0,0,0,3,1,0,0,1,4,0,0,1,1,0,0,0,0,0,0,0,0,0,1,1,0,1,0,0,0,1,1,1,0,0,1,0,1,1,0,0,0,1,1,1
ctflMM5586,1,1,1,1,0,0,2,0,0,2,2,0,1,0,0,0,0,0,1,3,1,0,1,0,0,0,1,0,1,0,?,0,1,1,0,1,1,0,0,1,0,0,0,0,0,0,?,?,1
cupreV1026,0,2,0,0,0,0,0,0,2,1,0,0,1,0,0,0,1,1,3,0,1,0,0,0,1,0,0,1,0,1,0,0,0,1,1,1,2,?,?,0,?,?,?,?,?,?,?,?
cuspMM4026,1,2,1,1,0,0,2,0,3,1,0,0,1,0,0,0,0,0,1,3,1,1,0,0,0,1,0,0,1,0,?,0,0,1,0,0,1,0,0,3,0,1,0,0,0,0,0,0,1
dintMM5505,1,2,0,1,0,0,1,0,2,1,0,0,1,0,0,0,0,0,1,3,1,1,0,0,0,1,0,1,1,0,?,0,1,1,0,0,1,0,0,0,0,1,0,0,0,0,0,0,3
dissitZ136,0,3,0,0,0,0,3,0,2,1,0,0,1,0,0,0,0,0,1,4,0,0,0,0,0,0,0,0,1,0,?,0,0,1,1,0,1,0,0,3,0,0,0,0,1,0,0,0,1
diversZ080,0,4,0,0,1,0,0,0,0,2,2,0,0,0,0,0,0,0,1,3,1,0,0,0,0,1,0,1,1,0,?,0,1,1,1,0,1,0,0,1,0,1,0,0,0,0,?,?,1
diversZ082,0,4,0,0,1,0,0,0,0,2,2,0,0,0,0,0,0,0,1,3,1,0,0,0,0,1,0,1,1,0,?,0,1,1,1,0,1,0,0,1,0,1,0,0,0,0,?,?,1
dmmagiZ152,1,1,0,1,0,1,0,0,2,1,0,0,1,0,1,0,0,1,1,1,1,1,0,0,0,0,0,0,1,3,1,0,1,1,0,0,1,0,0,1,0,1,0,0,0,0,0,0,0
dmmagiZ156,1,1,0,1,0,1,0,0,2,1,0,0,1,0,1,0,0,1,1,1,1,1,0,0,0,0,0,0,1,3,1,0,1,1,0,0,1,0,0,1,0,1,0,0,0,0,0,0,0
elatius,0,2,0,0,0,0,0,0,2,0,2,0,1,0,0,0,1,1,0,1,1,1,0,0,0,0,1,1,0,1,?,1,3,?,?,1,0,0,1,0,1,2,?,1,0,1,1,1
ericaeZ104,1,2,1,0,0,0,0,0,0,1,0,0,1,0,0,0,0,0,1,1,0,0,0,0,0,0,1,0,0,1,0,?,0,0,1,1,0,0,0,0,1,0,?,0,?,?,0,0,0,1
ericfoM89,1,2,1,0,0,0,0,0,0,1,0,0,1,0,0,0,0,0,1,1,0,0,0,0,0,0,1,0,0,1,0,?,0,0,1,1,0,0,0,0,1,0,1,0,?,?,0,0,0,1
euphoFF953,0,4,0,0,0,0,0,0,?,1,5,3,1,2,0,0,0,1,2,0,1,0,1,0,1,0,0,1,4,1,0,0,0,0,0,0,0,0,0,0,1,0,0,0,0,1,1,1
euprS13781,1,1,1,1,1,0,2,0,2,0,0,0,1,2,0,0,0,1,0,1,0,1,0,0,1,0,1,1,3,1,0,1,1,0,0,1,0,0,3,0,1,0,1,0,0,0,0,2

fallaxZ117,0,3,0,0,1,0,0,0,2,0,2,0,?,0,0,0,0,1,0,0,1,0,1,0,1,0,0,1,0,1,0,0,0,0,1,0,0,0,1,0,0,0,0,0,0,0,0,1

fatimuZ151,1,1,0,1,0,0,3,0,1,2,0,0,0,1,0,0,0,1,1,0,0,1,0,0,1,1,0,1,0,?,0,0,1,1,1,0,0,0,3,0,1,0,0,1,1,0,0,1

fatimuZ162,1,1,0,1,0,0,3,0,1,2,0,0,0,1,0,0,0,1,1,0,0,1,0,0,1,1,0,1,0,?,0,0,1,1,1,0,0,0,3,0,1,0,0,1,1,0,0,1

flexMM5046,1,2,0,1,1,0,1,0,1,2,1,0,0,0,2,1,1,1,0,1,1,1,1,1,1,0,1,1,3,1,0,1,0,0,0,1,0,0,1,0,0,0,0,0,0,0,0,1

flexuV1156,1,2,0,1,1,0,1,0,1,2,1,0,0,0,2,1,1,1,0,1,1,1,1,1,1,0,1,1,3,1,0,1,0,0,0,1,0,0,1,0,0,0,0,0,0,0,0,1

foliosuM41,1,4,0,0,0,0,0,0,3,1,0,0,1,0,0,0,0,1,0,0,1,0,0,1,1,0,1,1,0,1,0,0,0,1,1,0,2,0,1,0,0,0,?,0,0,0,0,1

fragilV912,1,1,1,0,1,1,0,1,0,0,4,0,1,3,0,1,0,1,0,0,0,1,0,0,0,2,0,0,1,0,2,0,0,0,1,0,0,1,1,0,0,3,1,1,1,0,0,1

fragMm4302,1,1,1,0,1,1,0,1,0,0,4,0,1,3,0,1,0,1,0,0,0,1,0,0,0,2,0,0,1,0,2,0,0,0,1,0,0,1,1,0,0,3,1,1,1,0,0,1

friNGB1616,1,2,1,1,0,0,2,0,?,1,0,0,0,1,0,0,1,1,0,1,0,1,0,0,0,0,0,1,0,?,0,1,1,1,0,1,0,0,1,0,0,0,1,0,0,0,0,1

friseFFCP3,1,2,1,1,0,0,2,0,?,1,0,0,0,1,0,0,1,1,0,1,0,1,0,0,0,0,0,1,0,?,0,1,1,1,0,1,0,0,1,0,0,0,1,0,0,0,0,1

funalFF732,1,1,1,0,1,0,3,0,1,0,3,0,0,0,0,0,0,1,0,1,1,4,1,0,1,0,0,1,0,1,0,1,3,1,0,1,0,0,1,0,1,2,1,0,0,0,0,2

galiodZ129,1,2,1,1,1,0,4,0,0,2,2,0,1,0,0,0,1,1,1,0,1,4,0,1,1,0,1,1,0,1,0,0,0,1,1,1,0,0,0,0,?,?,?,?,?,?,?,?

galioidM50,1,2,1,1,1,0,4,0,0,2,2,0,1,0,0,0,1,1,1,0,1,4,0,1,1,0,1,1,0,1,0,0,0,1,1,1,0,0,0,0,?,?,?,?,?,?,?,?

glomeruM46,1,2,0,0,0,0,1,0,0,0,0,0,1,0,0,0,0,1,4,0,1,0,1,0,0,0,1,1,0,1,0,0,0,1,0,0,0,0,1,0,0,0,0,0,0,0,0,1

glomerZ138,1,2,0,0,0,0,1,0,0,0,0,0,1,0,0,0,0,1,4,0,1,0,1,0,0,0,1,1,0,1,0,0,0,1,0,0,0,0,1,0,0,0,0,0,0,0,0,1

glomMM4767,1,2,0,0,0,0,2,0,0,0,0,0,1,0,0,0,0,1,4,0,1,0,1,0,0,0,1,1,0,1,0,0,0,1,0,0,0,0,1,0,0,0,0,0,0,0,0,

gnidiaZ116,1,2,1,1,0,1,2,0,2,1,0,0,1,1,1,1,0,1,0,1,1,1,0,1,0,0,1,1,0,1,0,1,0,1,0,1,1,1,0,0,1,0,1,0,0,0,0,1,1,1

gracileTLN,1,2,0,0,0,0,3,0,3,1,0,0,1,0,0,0,0,1,0,0,1,0,0,0,1,0,0,1,4,?,0,1,1,0,0,1,0,0,1,0,0,0,1,0,0,1,1,0

gracTTS424,1,2,0,0,0,0,3,0,3,1,0,0,1,0,0,0,0,1,0,0,1,0,0,0,1,0,0,1,4,?,0,1,1,0,0,1,0,0,1,0,0,0,1,0,0,1,1,0

gracV1054a,1,2,0,0,0,0,3,0,3,1,0,0,1,0,0,0,0,1,0,0,1,0,0,0,1,0,0,1,4,?,0,1,1,0,0,1,0,0,1,0,0,0,1,0,0,1,1,0

helichZ121,1,3,0,0,0,0,0,0,0,2,0,0,1,0,0,1,0,1,0,1,1,1,0,1,0,0,1,1,0,1,0,1,1,1,0,1,0,0,1,0,1,1,1,1,0,0,0,1

hilliaZ165,0,2,0,0,0,0,0,0,0,1,2,0,0,1,0,0,0,0,0,1,4,0,0,1,1,0,1,0,0,1,0,1,0,1,0,1,0,0,1,0,0,0,1,0,0,0,0,0,0,0,0,1

hirtum114,1,0,0,0,1,1,3,0,3,1,0,0,0,0,0,1,1,1,1,0,0,1,0,0,1,0,0,1,1,1,0,2,0,0,0,0,0,0,1,1,0,1,0,1,1,1,0,0,1

hispAB9440,0,3,0,0,1,1,0,0,2,1,0,0,0,0,0,1,1,1,1,0,1,1,2,0,1,0,0,1,1,0,1,0,1,3,1,0,1,0,0,1,0,1,0,1,0,0,1,1,2

hollanZ125,1,1,0,0,0,0,0,0,0,?,0,0,?,2,0,1,0,1,4,0,1,0,1,0,1,0,0,1,0,1,0,1,0,1,0,0,?,0,0,0,1,0,0,0,0,0,0,0,0,1

humiCh1881,2,2,0,1,0,0,1,0,?,1,0,1,1,1,0,0,0,1,0,0,1,0,0,0,0,0,0,0,1,0,1,1,0,0,0,0,0,0,0,1,0,0,0,1,0,0,?,?,0

humiNMW980,2,2,0,1,0,0,1,0,?,1,0,1,1,1,0,0,0,1,0,0,1,0,0,0,0,0,0,0,1,0,1,1,0,0,0,0,0,0,0,1,0,0,0,1,0,0,?,?,

humNMW4593,2,2,0,1,0,0,1,0,?,1,0,1,1,1,0,0,0,1,0,0,1,0,0,0,0,0,0,0,1,0,1,1,0,0,0,0,0,0,0,1,0,0,0,1,0,0,?,?

hystAB4642,0,2,0,1,1,1,2,0,1,2,1,0,0,1,0,1,0,1,0,0,0,1,1,0,1,0,0,1,3,?,0,0,1,1,0,1,0,0,1,0,1,0,0,0,0,0,0,1

hystS13648,1,2,0,1,1,0,2,0,1,2,1,0,0,1,0,1,0,1,0,0,0,1,1,0,1,0,0,1,3,?,0,0,1,1,0,1,0,0,1,0,1,0,0,0,0,0,0,1

imbTTS423,0,2,0,1,1,1,2,0,2,1,0,0,1,1,1,1,1,1,0,1,1,1,0,1,0,0,1,1,0,1,?,1,0,1,0,1,0,0,1,0,0,2,?,0,0,1,1,1

impediZ157,1,2,0,1,1,0,0,0,2,1,2,0,1,0,0,0,1,1,3,1,0,0,0,1,1,0,1,1,0,?,0,1,1,0,0,1,2,0,1,0,1,0,0,0,0,1,1,2
impedV1043,0,1,1,0,0,0,0,0,2,1,0,0,1,0,0,0,0,1,0,0,1,0,0,0,0,0,0,0,1,0,1,0,1,1,0,0,1,0,0,1,0,0,0,0,0,0,0,0,1
imprK36056,0,2,0,0,0,0,0,0,2,1,0,1,0,0,0,0,0,1,0,0,1,0,0,0,1,0,0,1,0,1,1,0,0,1,1,0,1,0,1,0,0,0,1,0,0,?,?,0
junciflM62,1,3,1,0,0,0,3,0,1,0,4,0,0,0,0,0,0,1,0,2,1,1,1,0,1,0,0,1,0,1,1,0,3,0,1,1,1,0,1,0,0,1,1,0,0,?,?,1
karooiZ160,0,2,0,0,1,0,0,0,0,1,2,0,1,0,0,0,0,1,0,2,1,2,0,1,1,0,1,1,0,?,0,1,1,1,0,1,0,0,1,0,1,1,0,0,0,0,0,0
lacinuZ135,0,2,0,0,1,0,2,0,1,2,2,0,0,0,0,0,0,1,0,0,1,1,1,0,1,0,0,1,0,1,0,0,5,1,0,1,0,0,1,0,1,0,1,0,0,0,0,1
leptoFF768,0,2,0,0,1,0,0,0,1,?,0,0,0,0,0,0,0,0,1,3,0,0,2,0,1,1,0,0,0,0,?,0,1,0,1,?,1,0,0,3,0,1,2,0,0,?,?,?,1
leptostFF1,1,0,1,0,1,1,3,0,3,1,0,0,0,0,1,1,1,1,0,0,1,0,0,1,0,0,1,1,1,0,2,0,0,0,0,0,0,1,1,0,1,0,1,1,1,0,0,1
limeriZ255,1,1,1,0,0,0,0,0,0,1,0,0,1,0,0,0,0,1,1,0,0,0,0,0,1,0,0,1,0,?,0,0,1,1,0,0,0,0,1,0,?,?,?,?,?,?,?,?
limfunZ254,1,1,1,0,1,0,3,0,1,0,3,0,0,0,0,0,0,1,0,1,1,4,1,0,1,0,0,1,0,1,0,1,3,1,0,1,0,0,1,0,1,2,1,0,0,0,0,2
limstrZ256,0,4,0,0,0,0,0,0,3,1,0,0,1,0,0,0,0,1,3,0,1,1,0,0,1,0,0,1,0,1,0,0,0,0,0,0,0,0,0,1,0,1,0,0,0,0,1,1,1
limstrZ264,0,4,0,0,0,0,0,0,3,1,0,0,1,0,0,0,0,1,3,0,1,1,0,0,1,0,0,1,0,1,0,0,0,0,0,0,0,0,0,1,0,1,0,0,0,0,1,1,1
lineaN4413,0,4,0,0,0,0,2,0,0,0,0,1,1,0,0,0,0,0,1,0,0,1,5,0,0,0,1,0,1,3,1,0,0,0,1,1,0,2,0,1,0,0,0,0,2,1,?,?,1
lineaN5509,0,4,0,0,0,0,2,0,0,0,0,1,1,0,0,0,0,0,1,0,0,1,5,0,0,0,1,0,1,3,1,0,0,0,1,1,0,2,0,1,0,0,0,0,2,1,1,1,1
lisamaZ105,1,2,1,0,1,0,3,0,1,0,3,0,0,0,0,0,0,1,4,1,1,4,1,0,1,0,0,1,0,1,0,1,3,1,0,1,0,0,1,0,1,2,1,0,0,0,0,2
litoS13464,1,2,0,0,1,0,0,0,2,2,0,0,1,0,0,0,0,0,1,0,1,1,1,0,0,1,0,0,1,0,?,0,1,1,0,0,1,0,0,1,0,1,0,0,0,0,0,0,1
lopolA1959,2,0,0,0,0,0,3,0,0,0,2,0,0,0,0,0,1,1,1,0,3,1,1,1,1,1,2,1,1,0,?,?,1,3,0,0,1,0,0,1,0,1,0,1,1,0,1,1,2
macrosM166,0,2,0,0,0,0,0,0,0,3,0,0,0,0,1,0,0,0,0,0,1,4,3,1,2,0,0,1,0,0,1,0,1,0,1,1,0,0,1,0,0,1,0,1,0,0,0,0,1,1,1
macrosM168,0,2,0,0,0,0,0,0,0,3,0,0,0,0,1,0,0,0,0,0,1,4,3,1,2,0,0,1,0,0,1,0,1,0,1,1,0,0,1,0,0,0,0,1,0,0,0,0,1,1,1
mauriN4844,2,2,1,1,1,1,1,0,3,0,0,0,0,0,0,1,0,0,1,0,0,1,0,0,0,0,0,0,0,1,0,1,0,0,3,1,0,0,0,0,1,0,1,0,1,1,0,?,?,1
mauriN5193,2,2,1,1,1,1,1,0,3,0,0,0,0,0,0,1,0,0,1,0,0,1,0,0,0,0,0,0,0,1,0,1,0,0,3,1,0,0,0,0,1,0,1,0,1,1,0,?,?,1
micpogZ029,0,3,0,0,1,0,3,0,2,0,0,0,1,0,0,0,0,0,1,0,1,0,1,0,0,1,0,0,1,0,?,0,1,1,1,0,1,0,0,3,0,1,0,0,0,0,0,0,1
microcZ106,1,2,1,1,0,0,1,1,?,?,?,?,?,?,?,?,?,?,1,?,0,0,?,?,?,?,?,?,?,?,1,0,?,0,0,0,1,0,0,1,1,0,0,3,0,1,1,0,0,1
micromZ113,1,2,1,1,0,0,0,0,0,1,2,0,0,1,1,0,0,0,1,3,1,1,1,0,0,0,0,0,0,1,0,1,0,1,1,0,0,1,0,0,1,0,1,0,0,0,0,0,0,0
microV1149,1,2,1,1,0,0,1,1,?,?,?,?,?,?,?,?,?,?,1,?,0,0,?,?,?,?,?,?,?,?,1,0,?,0,0,0,1,0,0,1,1,0,0,3,0,1,1,0,0,1
microV1150,1,2,1,1,0,0,1,1,?,?,?,?,?,?,?,?,?,?,1,?,0,0,?,?,?,?,?,?,?,?,1,0,?,0,0,0,1,0,0,1,1,0,0,3,0,1,1,0,0,1
minkwN5112,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,1,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,0,?,?,?,?,?,?,?,?
minusZ166,1,0,1,0,1,1,3,0,2,1,0,0,0,0,1,1,1,1,0,0,1,0,0,1,0,0,1,1,1,0,2,0,0,0,0,0,0,1,1,0,1,0,1,1,1,0
namaqFF896,1,2,1,1,0,0,0,0,2,0,0,0,0,0,0,0,0,0,1,4,0,1,1,0,0,0,1,0,1,0,0,0,0,0,0,1,1,0,0,0,1,0,0,0,1,0,0,1,1,1
namaquZ168,1,2,1,1,0,0,0,0,2,0,0,0,0,0,0,0,0,0,1,4,0,1,1,0,0,0,1,0,1,0,0,0,0,0,0,1,1,0,0,0,1,0,0,0,1,0,0,1,1,1
nautimonta,2,2,1,0,0,0,0,0,1,0,1,0,0,0,0,0,0,0,1,0,0,1,1,1,0,1,0,0,1,0,0,0,0,0,0,0,0,1,0,0,1,0,1,0,0,1,0,0,0,1

nickMM7540,1,2,0,1,1,0,1,0,1,2,1,0,0,0,2,1,1,1,0,0,1,1,1,1,1,0,1,1,5,1,0,0,0,0,1,0,0,0,3,0,1,0,0,0,0,0,0,1
nickreZ021,1,2,0,1,1,0,1,0,1,2,1,0,0,0,2,1,1,1,0,0,1,1,1,1,1,0,1,1,5,1,0,0,0,0,1,0,0,0,3,0,1,0,0,0,0,0,0,1
nickreZ148,1,2,0,1,1,0,1,0,1,2,1,0,0,0,2,1,1,1,4,0,1,1,1,1,1,0,1,1,5,1,0,0,0,0,1,0,0,0,3,0,1,0,0,0,0,0,0,1
nigrMM5559,1,1,0,1,0,0,3,0,1,2,0,0,0,1,0,0,0,1,1,0,0,1,0,0,1,1,0,1,0,?,0,0,1,1,1,0,0,0,3,0,1,0,0,1,1,0,0,1
nigroFF702,1,1,0,1,0,0,3,0,1,2,0,0,0,1,0,0,0,1,1,0,0,1,0,0,1,1,0,1,0,?,0,0,1,1,1,0,0,0,3,0,1,0,0,1,1,0,0,1
nudAB12249,1,2,0,1,1,0,4,0,1,2,2,0,0,0,0,0,0,1,3,0,1,1,0,0,1,0,0,1,3,1,0,1,0,1,1,0,2,0,1,0,0,0,0,0,0,0,0,1
nudicaZ131,1,2,0,1,1,0,4,0,1,2,2,0,0,0,0,0,0,1,3,0,1,1,0,0,1,0,0,1,3,1,0,1,0,1,1,0,2,0,1,0,0,0,0,0,0,0,0,1
occiMM4780,0,0,0,0,1,0,3,0,2,0,0,0,1,0,0,0,0,1,0,1,0,1,0,0,1,0,0,1,0,1,0,0,0,1,0,1,0,0,3,0,1,0,0,0,0,0,0,1
oresS14045,0,2,0,0,1,0,0,0,2,1,0,0,1,0,0,0,0,1,0,1,1,4,0,0,1,0,0,1,0,1,0,1,1,0,0,1,0,0,1,0,1,0,0,0,0,0,0,0
paniculM23,1,2,1,1,0,0,4,0,0,2,2,0,1,0,0,0,0,1,3,1,1,1,0,0,1,0,0,1,0,?,0,1,1,0,1,1,0,0,1,0,0,0,0,0,0,0,0,1
panicuZ100,1,2,1,1,0,0,4,0,0,2,2,0,1,0,0,0,0,1,3,1,1,1,0,0,1,0,0,1,0,?,0,1,1,0,1,1,0,0,1,0,0,0,0,0,0,0,0,1
paronyZ130,1,1,1,0,1,0,0,0,2,0,0,0,0,0,2,1,1,1,0,1,1,1,1,1,1,0,1,1,3,1,0,1,0,0,0,1,0,0,1,0,0,0,0,0,0,0,0,1
patulDGE25,1,2,1,0,1,0,0,0,2,0,0,0,1,0,0,0,0,1,4,1,1,4,0,1,1,0,1,1,0,?,0,1,1,0,0,1,0,0,3,0,1,0,0,0,0,1,1,1
patuluZ115,1,2,1,0,1,0,0,0,2,0,0,0,1,0,0,0,0,1,4,1,1,4,0,1,1,0,1,1,0,?,0,1,1,0,0,1,0,0,3,0,1,0,0,0,0,1,1,1
peniciZ112,0,4,0,0,1,0,0,0,2,0,0,0,1,0,0,0,0,1,0,0,0,0,0,0,1,0,1,1,0,?,0,0,0,0,1,0,0,0,1,0,1,0,0,0,0,1,1,1
penicV1140,?,4,0,0,1,0,0,0,2,0,0,0,1,0,0,0,0,1,0,0,0,0,0,0,1,0,1,1,0,?,0,0,0,0,1,0,0,0,1,0,1,0,0,0,0,1,1,1
pinifolM43,0,1,0,0,1,0,1,0,2,0,3,0,1,1,0,0,1,1,3,0,0,0,0,0,1,0,1,1,0,1,0,0,0,1,1,0,0,0,1,0,1,1,0,0,0,1,1,1
polycFF911,1,2,0,1,0,1,1,0,2,0,3,0,1,0,1,1,1,1,3,0,1,2,1,1,0,0,1,1,0,1,0,1,0,0,0,1,2,0,1,0,?,?,?,?,?,?,?,?
polycV1142,1,2,0,1,0,1,1,0,2,0,3,0,1,0,1,1,1,1,3,0,1,2,1,1,0,0,1,1,0,1,0,1,0,0,0,1,2,0,1,0,?,?,?,?,?,?,?,?
polygaZ097,0,2,0,0,0,0,0,0,0,2,2,0,0,1,0,0,0,1,4,0,0,0,1,0,1,0,0,1,0,1,0,0,0,1,0,1,0,0,1,0,1,0,0,1,0,0,0,1
polygaZ098,0,2,0,0,0,0,0,0,0,2,2,0,0,1,0,0,0,1,4,0,0,0,1,0,1,0,0,1,0,2,0,0,0,1,0,1,0,0,1,0,1,0,0,0,0,0,0,1
procK36061,2,2,1,0,0,0,0,0,?,0,0,0,1,0,0,0,0,1,0,0,1,1,0,0,0,0,0,1,0,1,3,1,0,1,0,1,2,0,1,0,1,0,1,0,0,?,?,1
prostrZ081,1,1,1,1,0,1,0,0,2,1,0,0,1,1,0,0,0,1,3,0,0,0,0,1,1,0,0,1,0,?,0,0,?,?,?,?,?,?,?,0,?,?,?,?,?,?,?,?
prostrZ086,1,1,1,1,0,0,0,0,2,1,0,0,1,1,0,0,0,1,3,0,0,0,0,1,1,0,0,1,0,?,0,0,0,0,0,0,0,0,1,0,1,0,1,0,0,?,?,1
prostrZ089,1,1,1,1,0,0,0,0,2,1,0,0,1,1,0,0,0,1,3,0,0,0,0,1,1,0,0,1,0,?,0,0,?,?,?,?,?,?,?,0,?,?,?,?,?,?,?,?
pseudoZ078,1,1,1,1,0,0,2,0,1,2,2,0,0,0,0,0,0,1,0,0,0,1,0,0,1,0,0,1,0,1,0,0,0,1,1,1,2,0,1,0,0,0,0,1,0,1,1,1
pseudoZ087,1,1,1,1,0,0,2,0,1,2,2,0,0,0,0,0,0,1,0,0,0,1,0,0,1,0,0,1,0,1,0,0,0,1,1,1,2,0,1,0,0,0,0,1,0,1,1,1
pseuMB1904,1,1,1,1,0,0,2,0,1,2,2,0,0,0,0,0,0,1,0,0,0,1,0,0,1,0,0,1,0,1,0,0,0,1,1,1,2,0,1,0,0,0,0,1,0,1,1,1
pubeMM4798,1,2,0,1,1,1,2,0,2,1,0,0,1,0,1,1,0,1,3,1,1,1,0,1,0,0,0,1,0,1,0,1,1,0,0,1,0,0,1,0,0,0,0,0,0,0,0,0,
pubescFCP4,1,2,0,1,1,1,2,0,2,1,0,0,1,0,1,1,0,1,3,1,1,1,0,1,0,0,0,1,0,1,0,1,1,0,0,1,0,0,1,0,0,0,0,0,0,0,0,0
pungeV1340,0,3,0,1,1,0,4,0,2,0,3,0,0,2,0,0,0,1,0,0,1,1,0,0,0,0,0,0,1,0,1,0,0,0,1,1,0,0,0,1,0,1,0,?,0,0,0,0,1

pycnMNB082,1,2,0,1,0,0,1,0,3,1,3,0,0,0,0,0,1,1,3,1,1,1,0,0,1,0,1,1,0,1,0,1,1,1,0,1,0,0,1,0,1,1,0,0,0,1,1,
quartzZ026,1,1,1,0,0,1,0,0,1,0,4,0,1,3,0,1,0,1,0,0,0,1,0,0,0,2,0,0,1,0,2,0,0,0,1,0,0,1,1,0,0,3,1,1,1,0,0,1
quartzZ150,1,1,1,0,0,1,0,0,1,0,4,0,1,3,0,1,0,1,0,0,0,1,0,0,0,2,0,0,1,0,2,0,0,0,1,0,0,1,1,0,0,3,1,1,1,0,0,1
quinMM4238,0,2,0,0,1,0,0,0,2,1,0,0,0,0,0,0,0,1,3,0,0,0,0,1,1,0,0,1,0,1,0,0,1,1,0,0,0,0,1,0,0,0,0,0,0,1,1,1
racemoZ128,2,?,1,1,0,0,1,0,3,1,0,0,0,0,0,0,0,1,4,2,1,3,0,0,1,0,0,1,0,1,0,0,3,0,1,1,2,0,1,0,?,?,?,?,?,?,?,?
radiK36062,2,0,1,1,0,1,1,0,2,1,0,1,0,0,2,1,0,1,0,0,1,5,1,1,1,0,0,1,0,1,1,1,0,1,1,1,0,0,1,0,0,0,1,1,1,0,0,0
rariflM100,1,?,1,1,1,0,1,0,0,0,3,0,1,0,0,0,?,1,0,1,1,1,0,0,1,0,0,1,0,?,?,1,5,1,1,1,0,0,1,0,1,1,?,0,0,?,?,1
retamN5559,2,3,1,0,0,0,0,0,1,0,4,0,1,3,0,0,0,1,0,0,1,1,1,0,1,2,0,1,0,0,3,0,5,0,1,0,0,0,1,1,0,0,0,2,1,?,?,1
rhizomZ153,2,0,1,0,1,0,0,0,0,1,0,0,1,0,0,0,0,1,3,0,1,1,0,0,0,0,0,1,0,1,0,0,0,1,0,0,0,0,3,0,1,0,0,0,0,0,0,1
rhizomZ156,2,0,1,0,1,0,0,0,0,1,0,0,1,0,0,0,0,1,3,0,1,1,0,0,0,0,0,1,0,1,0,0,0,1,0,0,0,0,3,0,1,0,0,0,0,0,0,1
rufeS14093,0,2,0,0,1,0,0,0,0,1,2,0,1,0,0,0,1,1,0,1,0,0,0,0,0,0,0,1,0,?,0,1,1,0,0,1,0,0,1,0,1,0,0,0,0,0,0,0
scabruM155,0,3,0,0,1,1,0,0,2,1,0,0,0,0,1,1,1,1,0,1,1,3,0,1,0,0,1,1,0,1,0,1,3,1,0,1,0,0,1,0,1,0,1,0,0,1,1,2
scandeZ134,1,2,1,1,1,0,4,0,3,1,2,0,1,1,0,0,0,1,3,0,1,1,0,0,1,0,0,1,0,?,0,0,1,1,1,0,2,0,1,0,1,1,0,0,0,0,0,1
schwK36066,1,2,0,0,1,0,0,0,4,1,0,1,0,0,0,0,1,1,0,0,1,0,0,0,1,0,0,1,0,1,1,0,1,0,0,0,0,0,1,0,1,0,1,0,1,?,?,1
scirMM5515,0,2,0,0,0,0,0,0,0,2,0,0,1,0,0,0,0,1,4,1,1,1,0,0,1,0,0,1,0,1,0,1,1,0,0,1,0,0,0,0,1,0,0,0,0,1,1,1
sedifoM146,1,2,0,0,1,0,0,0,3,1,0,0,1,4,0,0,1,1,0,0,0,0,0,0,0,0,0,1,1,0,1,0,0,0,1,1,1,0,0,1,0,1,1,0,0,0,1,1,1
sertulZ095,1,2,0,0,0,0,0,0,0,2,2,0,0,0,0,0,0,0,1,0,0,0,0,0,1,0,1,0,0,1,0,1,0,0,0,1,0,1,0,0,1,0,0,0,0,1,0,1,1,1
sonderZ122,0,3,0,0,1,1,0,0,2,1,0,0,0,5,1,1,1,1,0,1,1,1,0,1,0,0,1,1,0,?,?,1,3,1,0,?,?,0,1,0,1,1,?,1,0,1,1,1
spicaFF850,1,2,1,0,1,0,3,0,3,1,0,0,1,0,0,0,0,1,4,1,1,4,0,1,1,0,1,1,0,?,0,1,1,0,0,1,0,0,3,0,1,0,0,0,0,0,0,1
spicaFF950,1,2,1,0,1,0,3,0,3,1,0,0,1,0,0,0,0,1,4,1,1,4,0,1,1,0,1,1,0,?,0,1,1,0,0,1,0,0,3,0,1,0,0,0,0,0,0,1
spicaV1300,1,2,1,0,1,0,3,0,3,1,0,0,1,0,0,0,0,1,4,1,1,4,0,1,1,0,1,1,0,?,0,1,1,0,0,1,0,0,3,0,1,0,0,0,0,0,0,1
spinulM148,0,2,0,1,1,0,4,0,2,0,3,0,0,2,0,0,0,1,0,0,1,1,0,0,0,0,0,0,1,0,1,0,0,0,1,1,0,0,0,1,0,1,0,?,0,0,0,0,1
spMM4121,0,3,0,0,1,0,0,0,3,1,0,0,1,0,0,0,1,1,3,0,1,1,0,1,0,0,1,1,0,?,0,1,1,1,?,1,0,0,1,0,1,0,0,0,0,1,1,0
spMM4733,1,1,1,1,0,0,0,0,3,1,3,0,1,1,1,0,0,1,3,2,0,3,1,0,0,0,0,1,0,?,0,1,1,0,0,?,0,0,1,0,1,0,0,1,0,1,1,0
spMM7535,1,2,1,0,1,0,3,0,3,1,0,0,1,0,0,0,0,1,4,1,1,4,0,1,1,0,1,1,0,?,0,1,1,0,0,1,0,0,3,0,1,0,0,0,0,0,0,1
spMM7536,1,2,1,0,1,0,3,0,3,1,0,0,1,0,0,0,0,1,4,1,1,4,0,1,1,0,1,1,0,?,0,1,1,0,0,1,0,0,3,0,1,0,0,0,0,0,0,1
spS13369,0,?,0,0,1,?,0,?,3,1,0,?,1,0,0,0,1,1,3,0,1,1,0,1,?,0,1,1,0,?,0,1,1,1,?,1,0,0,1,0,1,0,0,0,0,?,?,?
spS13426,1,2,0,1,0,1,1,0,2,0,3,0,1,0,1,1,1,1,3,0,1,2,1,1,0,0,1,1,0,1,0,1,0,0,0,1,2,0,1,0,?,?,?,?,?,?,?,?
spS13493,1,2,0,1,1,0,0,0,2,1,2,0,1,0,0,0,1,1,3,1,0,0,0,1,1,0,1,1,0,?,0,1,1,0,0,1,2,0,1,0,1,0,0,0,0,1
spS14151,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,1,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,0,?,?,?,?,?,?,?,?
spTEMV1290,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,1,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,?,0,?,?,?,?,?,?,?,?

spZ032,0,1,0,0,1,1,3,0,2,1,0,0,0,0,1,1,1,1,0,1,1,0,0,1,0,0,1,1,0,1,0,1,3,1,0,1,0,0,1,0,1,0,1,0,0,1,1,2

spZ076,0,2,0,0,1,0,0,0,2,1,2,0,1,0,0,0,1,1,3,1,0,0,0,1,1,0,1,1,0,?,0,1,1,0,0,1,2,0,1,0,1,0,0,0,0,1,1,2

spZ077,1,1,0,1,0,0,0,0,1,2,0,0,1,1,0,0,0,1,3,1,1,1,0,0,0,0,0,1,3,1,0,1,1,0,0,1,0,0,1,0,1,0,0,0,0,0,0,0

spZ084,1,2,0,0,1,0,0,0,3,?,0,0,?,0,0,0,0,1,0,1,0,1,0,1,0,0,0,1,0,?,0,1,1,1,?,1,0,0,1,0,1,0,0,0,0,?,?,0

spZ091,0,2,0,0,0,0,0,0,2,?,0,0,?,0,0,0,0,1,0,2,0,0,0,0,0,0,0,1,0,?,0,0,0,0,?,0,0,0,3,0,1,0,0,0,0,?,?,1

spZ092,0,2,1,1,1,0,3,0,2,2,0,0,1,0,0,0,0,0,1,3,1,0,1,0,1,1,0,1,1,0,?,0,1,1,1,0,1,0,0,1,0,1,0,0,0,0,1,1,1

spZ096,0,2,1,0,1,0,0,0,0,1,2,0,1,0,0,0,0,0,1,0,0,0,1,0,0,0,0,0,0,1,0,?,0,0,0,1,1,0,0,0,1,0,0,0,0,0,0,?,?,1

spZ099,0,2,0,0,0,0,1,0,0,1,0,0,1,0,0,0,0,0,1,1,0,0,0,0,1,2,0,1,1,0,?,0,0,0,0,?,1,0,0,?,0,1,o,0,0,0,?,?,1

spZ155,1,2,1,0,0,0,0,0,0,1,0,0,1,0,0,0,0,0,1,1,0,0,0,0,0,0,1,0,0,1,0,?,0,0,1,1,0,0,0,0,1,0,?,?,?,?,?,?,?,?

spZ158,0,2,0,0,1,0,0,0,1,2,1,0,0,0,0,0,0,0,1,3,0,0,1,1,1,1,0,0,0,0,?,0,1,0,1,0,1,0,0,3,0,1,0,0,0,0,?,?,1

spZ164,1,2,1,1,1,0,0,0,0,1,0,0,1,0,0,0,0,0,1,1,0,0,0,0,0,0,1,0,0,1,0,?,0,0,1,1,0,0,0,0,1,0,?,?,?,0,?,?,?,?

squarFF851,1,2,1,1,1,0,4,0,3,1,0,0,1,0,0,0,0,1,1,0,1,0,0,0,1,0,0,1,0,1,0,0,0,0,0,0,0,0,0,1,0,1,1,0,0,0,0,0,4

squarrZ123,1,2,1,1,1,0,4,0,3,1,0,0,1,0,0,0,0,1,1,0,1,0,0,0,1,0,0,1,0,1,0,0,0,0,0,0,0,0,0,1,0,1,1,0,0,0,0,0,4

stellN4848,?,?,?,?,?,0,?,?,?,0,0,0,0,3,0,0,0,1,0,1,1,1,0,0,0,0,0,0,1,0,1,3,0,2,1,1,0,0,0,1,0,?,?,?,?,?,?,?,?

strictuM48,0,4,0,0,0,0,0,0,0,3,1,0,0,1,0,0,0,0,0,1,3,0,1,1,0,0,1,0,0,1,0,1,0,1,0,0,0,0,0,0,0,0,0,1,0,1,0,0,0,0,0,1,1,1

stricV1295,0,4,0,0,0,0,0,0,0,3,1,0,0,1,0,0,0,0,0,1,3,0,1,1,0,0,1,0,0,1,0,1,0,1,0,0,0,0,0,0,0,0,0,1,0,1,0,0,0,0,0,1,1,1

striMM5562,0,2,0,0,1,0,0,0,3,0,0,0,1,0,0,0,0,0,1,0,1,0,1,0,0,1,0,1,1,0,1,0,1,1,0,0,1,0,0,0,0,1,0,0,0,0,0,0,0

strvirZ269,0,2,0,0,1,0,1,0,?,1,2,0,1,3,0,1,1,1,0,0,1,1,0,1,0,0,1,1,0,0,0,0,0,0,0,1,0,0,1,0,1,0,1,0,0,0,0,1

subnuduM96,0,2,0,0,1,0,3,0,2,2,0,0,1,0,0,0,0,0,1,3,1,0,1,0,1,1,0,1,1,0,?,0,1,1,1,0,1,0,0,3,0,1,0,0,0,0,0,1,1,1

subsuN4374,2,2,0,0,0,0,3,0,2,2,0,0,1,0,0,0,0,0,1,3,0,0,1,0,1,1,0,1,1,0,?,0,1,1,1,0,1,0,0,3,1,0,0,0,2,1,1,1,1

susannZ127,0,4,0,0,0,0,0,0,0,3,1,0,0,1,1,0,0,0,1,0,0,1,0,0,1,1,0,1,1,0,1,0,0,0,1,1,0,2,0,1,0,0,0,?,0,0,0,0,1

tepuK36057,0,?,1,1,0,0,0,0,?,2,0,1,0,0,0,0,0,0,1,0,0,1,0,0,0,1,0,0,1,0,1,1,0,0,0,1,0,0,0,1,0,0,0,1,0,1,?,?,1

translZ090,1,2,0,0,1,0,0,0,2,1,0,0,1,0,0,0,1,1,0,0,1,2,1,1,0,0,1,1,0,?,0,1,1,1,0,0,0,0,1,0,1,0,0,0,0,1,1,0

trifloM128,1,2,1,1,1,0,4,0,2,1,0,0,1,0,0,0,0,0,1,4,0,1,0,1,0,0,0,0,1,0,1,0,0,0,0,0,1,0,0,1,0,1,0,0,0,0,1,1,1

trifloZ137,1,2,1,1,1,0,4,0,2,1,0,0,1,0,0,0,0,0,1,4,0,1,0,1,0,0,0,0,1,0,1,0,0,0,0,0,1,0,0,1,0,1,0,0,0,0,1,1,1

trvaB15178,1,0,1,1,0,1,1,0,0,1,0,0,0,0,1,1,0,1,0,?,1,3,0,0,1,0,0,1,0,?,?,1,3,0,0,1,2,0,1,0,1,2,?,0,0,1,1,1

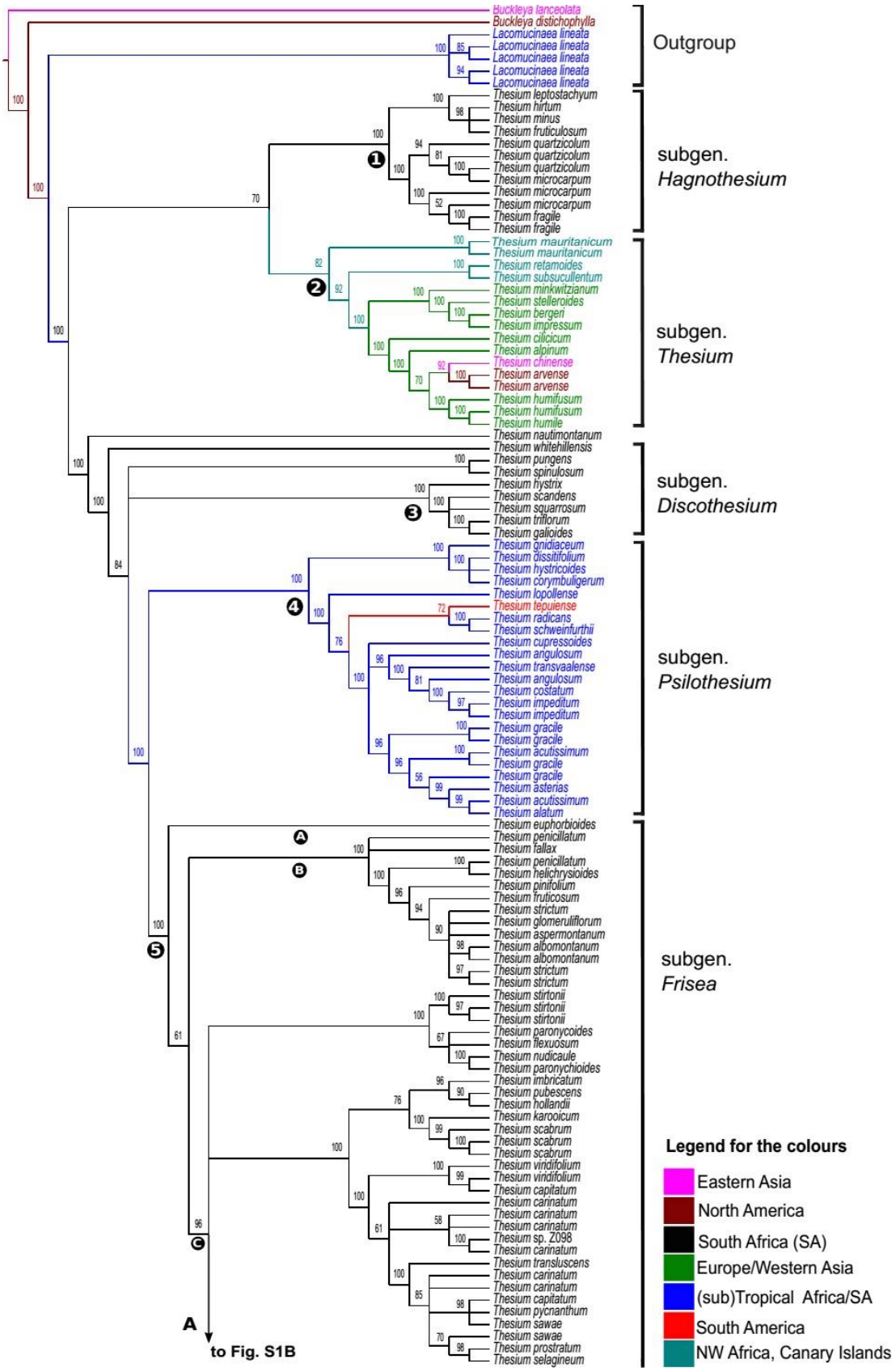
urcelH7329,1,2,1,1,0,0,1,0,0,0,0,0,0,0,0,0,0,0,1,0,1,1,1,0,0,1,0,0,1,0,1,?,1,5,0,0,1,0,0,1,0,1,1,?,0,2,1,1,1

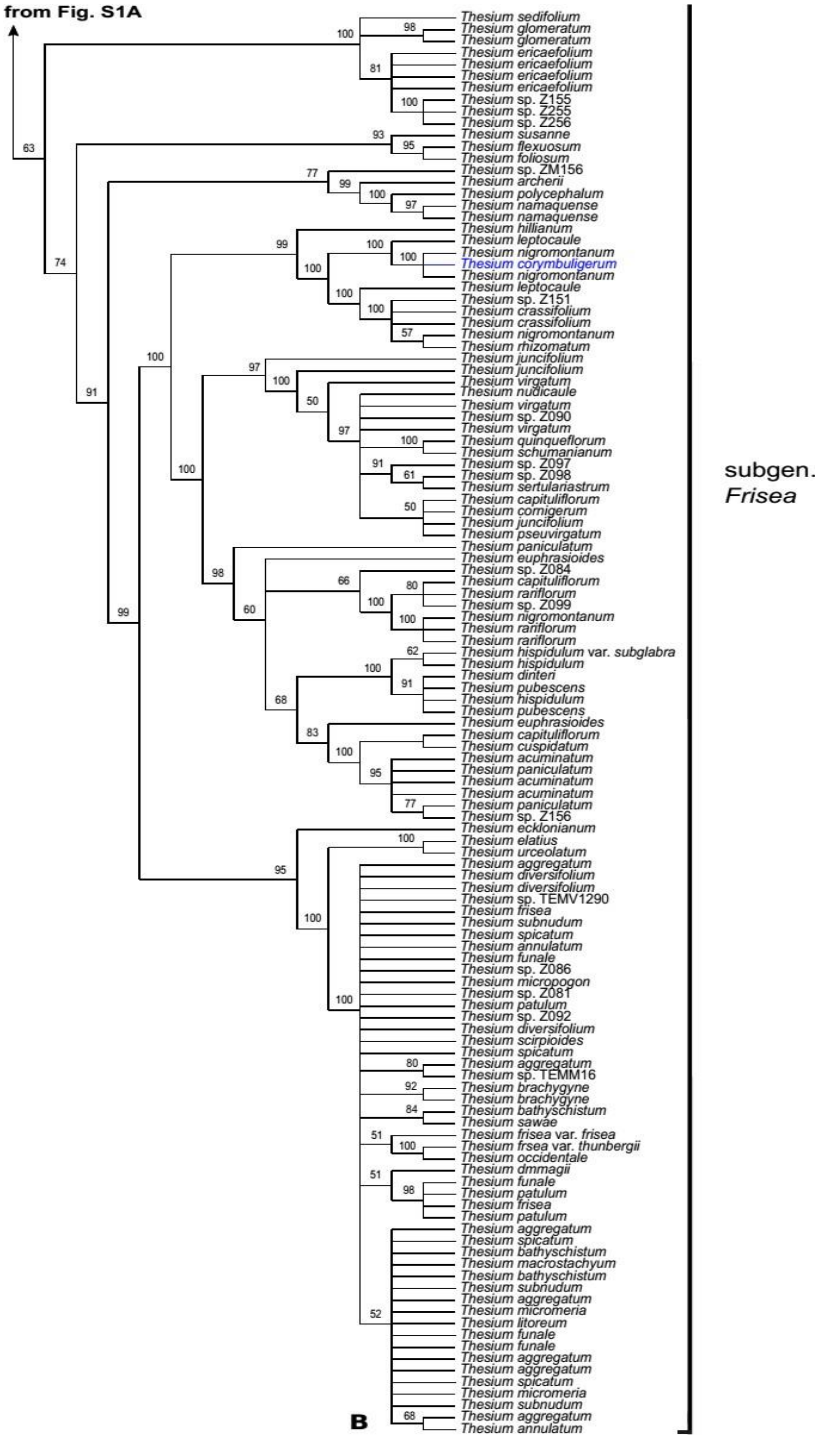
virgatZ102,1,1,1,1,0,0,2,0,1,2,2,0,0,0,0,0,0,0,1,0,0,0,1,0,0,1,0,0,1,0,1,0,0,0,1,1,1,2,0,1,0,0,0,0,1,0,1,1,1

virgaV1153,1,2,1,0,0,0,2,0,0,2,2,0,0,0,0,0,0,0,1,0,0,0,1,0,0,1,0,0,1,5,1,0,0,0,1,1,1,2,0,1,0,0,0,0,1,0,1,1,1

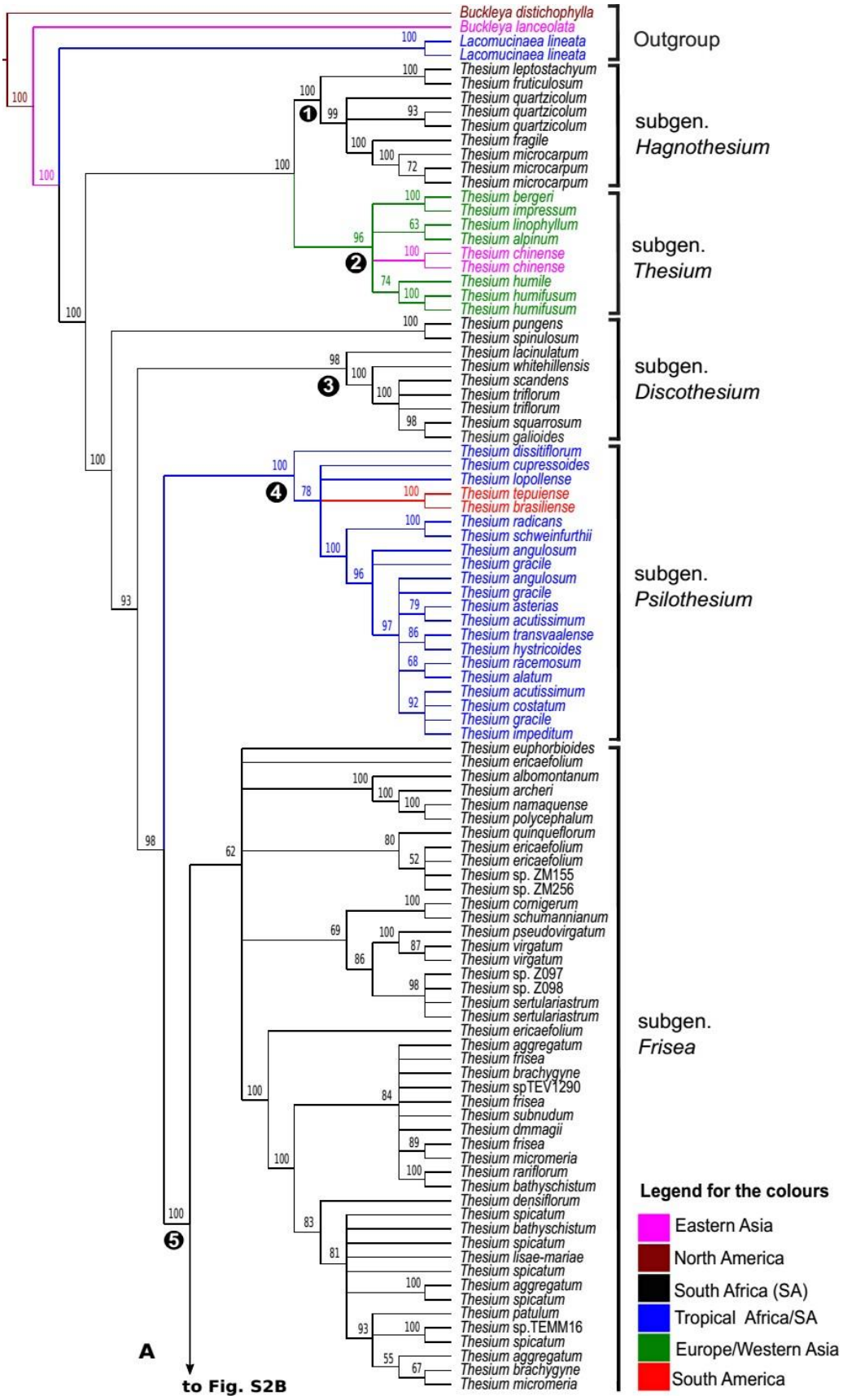
viridFF680,0,3,0,0,0,0,0,0,0,2,1,0,0,1,0,0,0,0,0,1,0,1,0,0,0,1,1,0,1,1,0,1,0,1,1,0,0,1,0,0,1,0,0,0,1,0,0,1,1,0

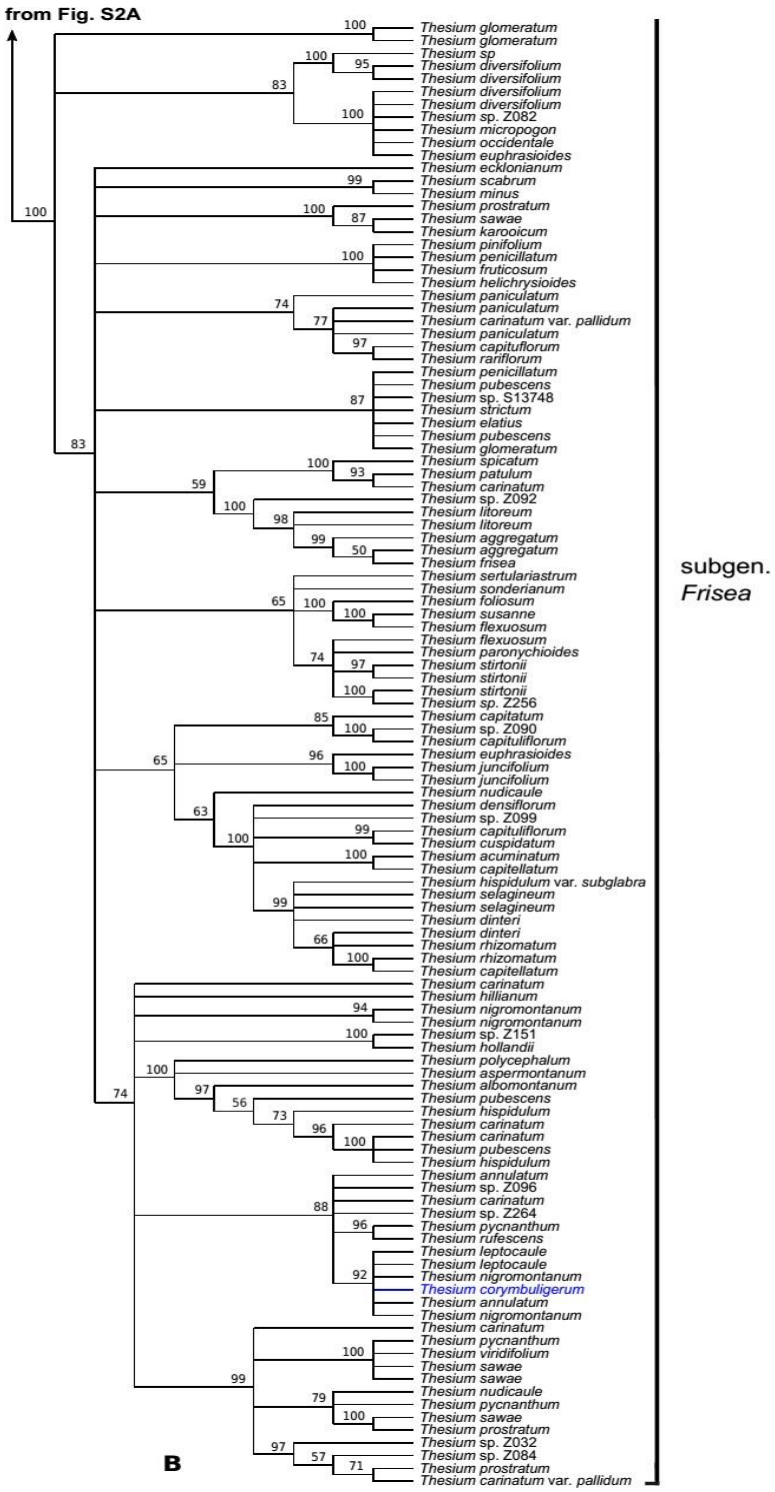
whitehZ161,1,2,1,1,1,0,3,0,0,1,0,0,0,1,0,0,0,1,4,0,1,1,0,0,1,0,1,1,0,?,0,0,1,1,0,0,0,0,3,0,1,0,0,0,0,0,0,2


Buckleya lanceolata
Buckleya distichophylla
Lacomucinaea lineata
Lacomucinaea lineata
Lacomucinaea lineata
Lacomucinaea lineata
Lacomucinaea lineata
Outgroup
Thesium leptostachyum
Thesium hirtum
Thesium minus
Thesium fruticulosum
Thesium quartzicolum
Thesium quartzicolum
Thesium quartzicolum
Thesium microcarpum
Thesium microcarpum
Thesium microcarpum
Thesium fragile
Thesium fragile
subgen.
Hagnothesium
Thesium mauritanicum
Thesium mauritanicum
Thesium retamoides
Thesium subsucullentum
Thesium minkwitzianum
Thesium stelleroides
Thesium bergeri
Thesium impressum
Thesium cilicicum
Thesium alpinum
Thesium chinense
Thesium arvense
Thesium arvense
Thesium humifusum
Thesium humifusum
Thesium humile
subgen.
Thesium
Thesium nautimontanum
Thesium whitehillensis
Thesium pungens
Thesium spinulosum
Thesium hystrix
Thesium scandens
Thesium squarrosum
Thesium trifforum
Thesium galioides
subgen.
Discothesium
Thesium gnidiaceum
Thesium dissitifolium
Thesium hystricoides
Thesium corymbuligerum
Thesium lopollense
Thesium tepuiense
Thesium radicans
Thesium schweinfurthii
Thesium cupressoides
Thesium angulosum
Thesium transvaalense
Thesium angulosum
Thesium costatum
Thesium impeditum
Thesium impeditum
Thesium gracile
Thesium gracile
Thesium acutissimum
Thesium gracile
Thesium gracile
Thesium asterias
Thesium acutissimum
Thesium alatum
subgen.
Psilothesium
Thesium euphorbioides
Thesium penicillatum
Thesium fallax
Thesium penicillatum
Thesium helichrysioides
Thesium pinifolium
Thesium fruticosum
Thesium strictum
Thesium glomeruliflorum
Thesium aspermontanum
Thesium albomontanum
Thesium albomontanum
Thesium strictum
Thesium strictum
Thesium stirtonii
Thesium stirtonii
Thesium stirtonii
Thesium paronycoides
Thesium flexuosum
Thesium nudicaule
Thesium paronychioides
Thesium imbricatum
Thesium pubescens
Thesium hollandii
Thesium karooicum
Thesium scabrum
Thesium scabrum
Thesium scabrum
Thesium viridifolium
Thesium viridifolium
Thesium capitatum
Thesium carinatum
Thesium carinatum
Thesium sp. Z098
Thesium carinatum
Thesium transluscens
Thesium carinatum
Thesium carinatum
Thesium capitatum
Thesium pycnanthum
Thesium sawae
Thesium sawae
Thesium prostratum
Thesium selagineum
subgen.
Frisea
A
to Fig. S1B
Legend for the colours
Eastern Asia
North America
South Africa (SA)
Europe/Western Asia
(sub)Tropical Africa/SA
South America
NW Africa, Canary Islands

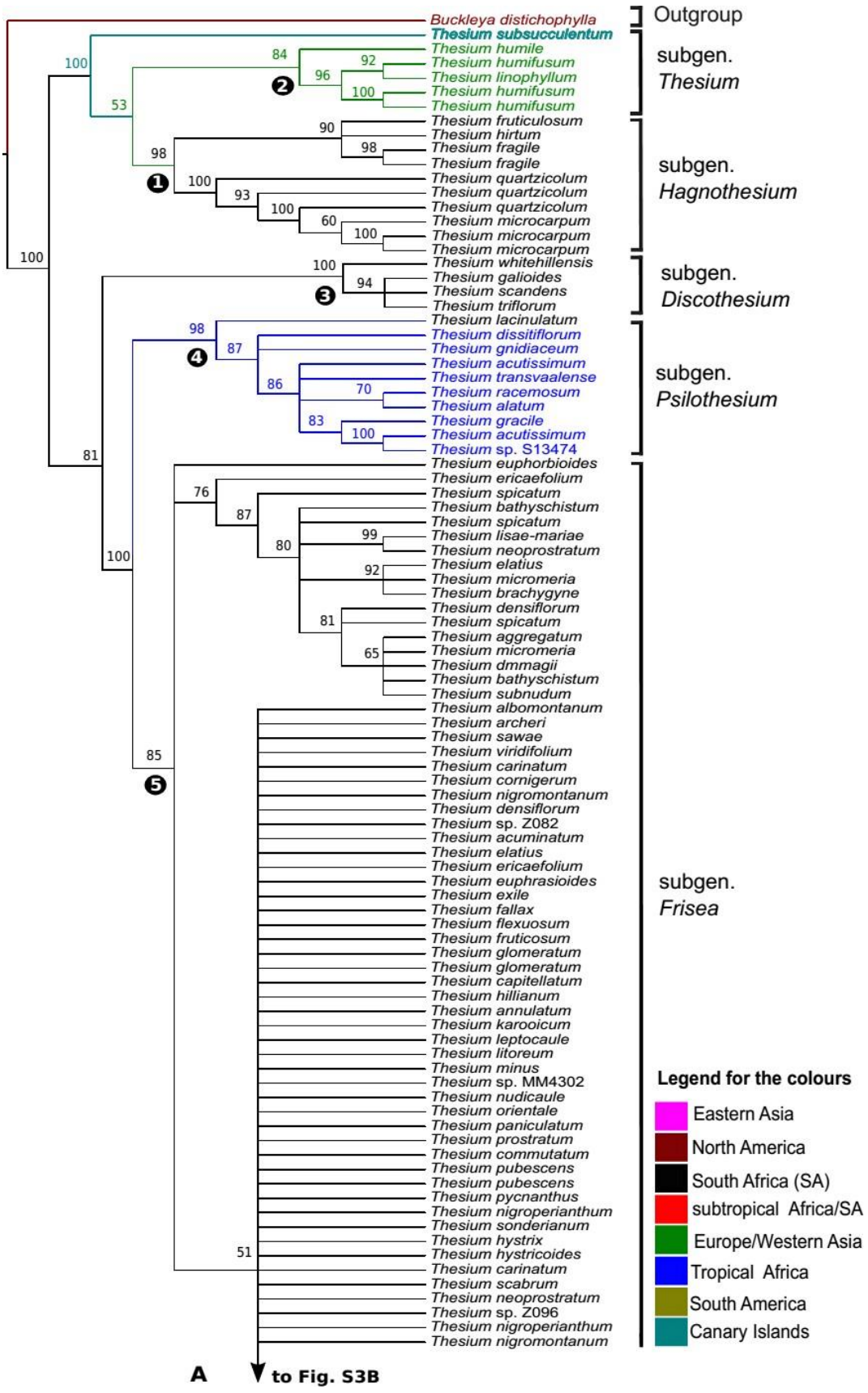


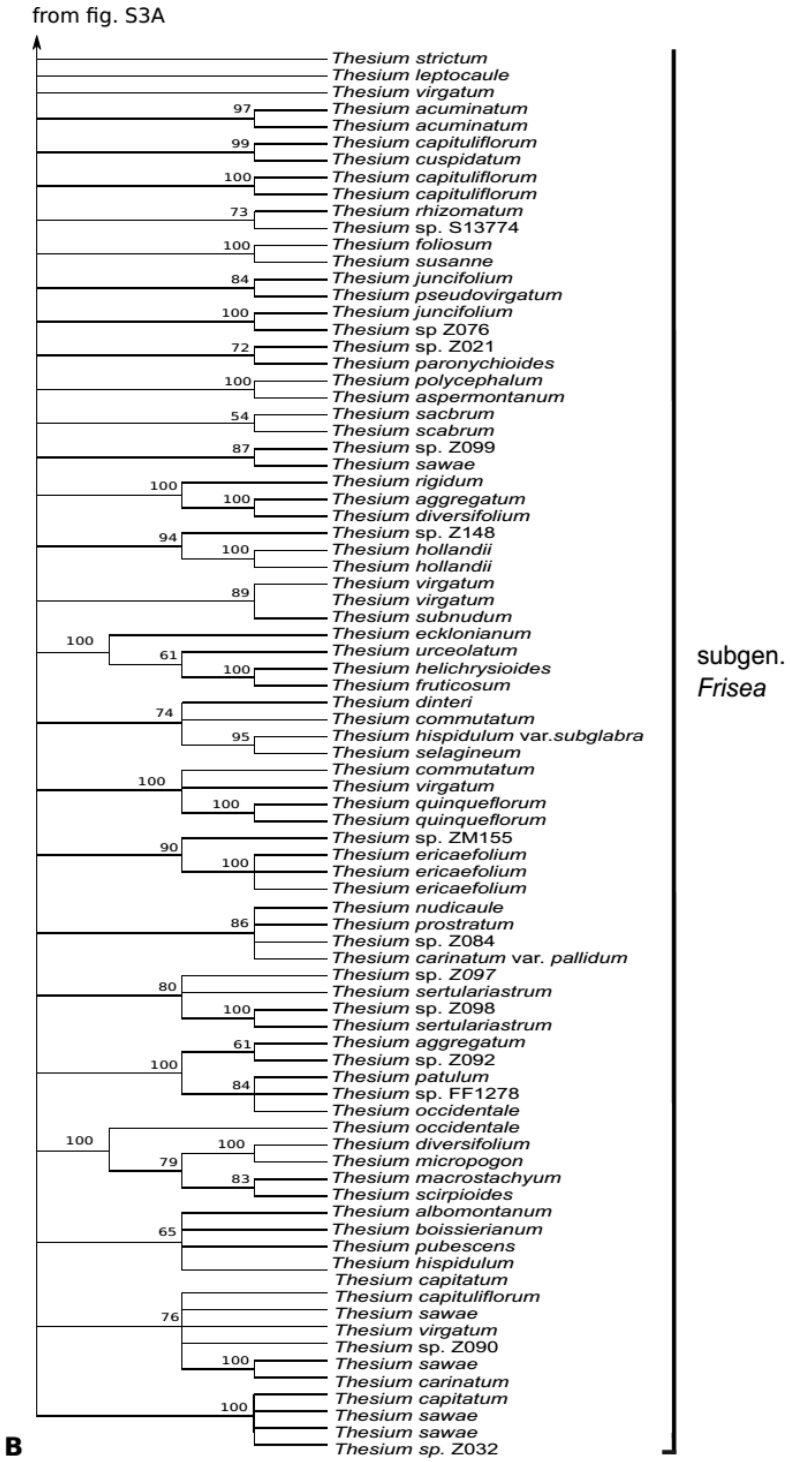

**Appendix Fig. S2.1 (A and B):** The 50% majority-rule phylogenetic tree obtained from the Bayesian analysis of 234 taxa used for the ITS data set. Numbers above each branch represent the percentage posterior probabilities (> 60%). Coloured leaves and taxa names show geographical range estimates of species. Numbers 1–5 and letters A–E indicate nodes discussed in the text.


Buckleya distichophylla
Buckleya lanceolata
Lacomucinaea lineata
Lacomucinaea lineata
Outgroup
Thesium leptostachyum
Thesium fruticulosum
Thesium quartzicolum
Thesium quartzicolum
Thesium quartzicolum
Thesium fragile
Thesium microcarpum
Thesium microcarpum
Thesium microcarpum
subgen.
Hagnothesium
Thesium bergeri
Thesium impressum
Thesium linophyllum
Thesium alpinum
Thesium chinense
Thesium chinense
Thesium humile
Thesium humifusum
Thesium humifusum
subgen.
Thesium
Thesium pungens
Thesium spinulosum
Thesium lacinulatum
Thesium whitehillensis
Thesium scandens
Thesium triflorum
Thesium triflorum
Thesium squarrosum
Thesium galioides
subgen.
Discothesium
Thesium dissitiflorum
Thesium cupressoides
Thesium lopollense
Thesium tepuiense
Thesium brasiliense
Thesium radicans
Thesium schweinfurthii
Thesium angulosum
Thesium gracile
Thesium angulosum
Thesium gracile
Thesium asterias
Thesium acutissimum
Thesium transvaalense
Thesium hystricoides
Thesium racemosum
Thesium alatum
Thesium acutissimum
Thesium costatum
Thesium gracile
Thesium impeditum
subgen.
Psilothesium
Thesium euphorbioides
Thesium ericaefolium
Thesium albomontanum
Thesium archeri
Thesium namaquense
Thesium polycephalum
Thesium quinqueflorum
Thesium ericaefolium
Thesium ericaefolium
Thesium sp. ZM155
Thesium sp. ZM256
Thesium cornigerum
Thesium schumannianum
Thesium pseudovirgatum
Thesium virgatum
Thesium virgatum
Thesium sp. Z097
Thesium sp. Z098
Thesium sertulariastrum
Thesium sertulariastrum
Thesium ericaefolium
Thesium aggregatum
Thesium frisea
Thesium brachygyne
Thesium spTEV1290
Thesium frisea
Thesium subnudum
Thesium dmmagii
Thesium frisea
Thesium micromeria
Thesium rariflorum
Thesium bathyschistum
Thesium densiflorum
Thesium spicatum
Thesium bathyschistum
Thesium spicatum
Thesium lisae-mariae
Thesium spicatum
Thesium aggregatum
Thesium spicatum
Thesium patulum
Thesium sp.TEMM16
Thesium spicatum
Thesium aggregatum
Thesium brachygyne
Thesium micromeria
subgen.
Frisea
Legend for the colours
Eastern Asia
North America
South Africa (SA)
Tropical Africa/SA
Europe/Western Asia
South America
A
to Fig. S2B

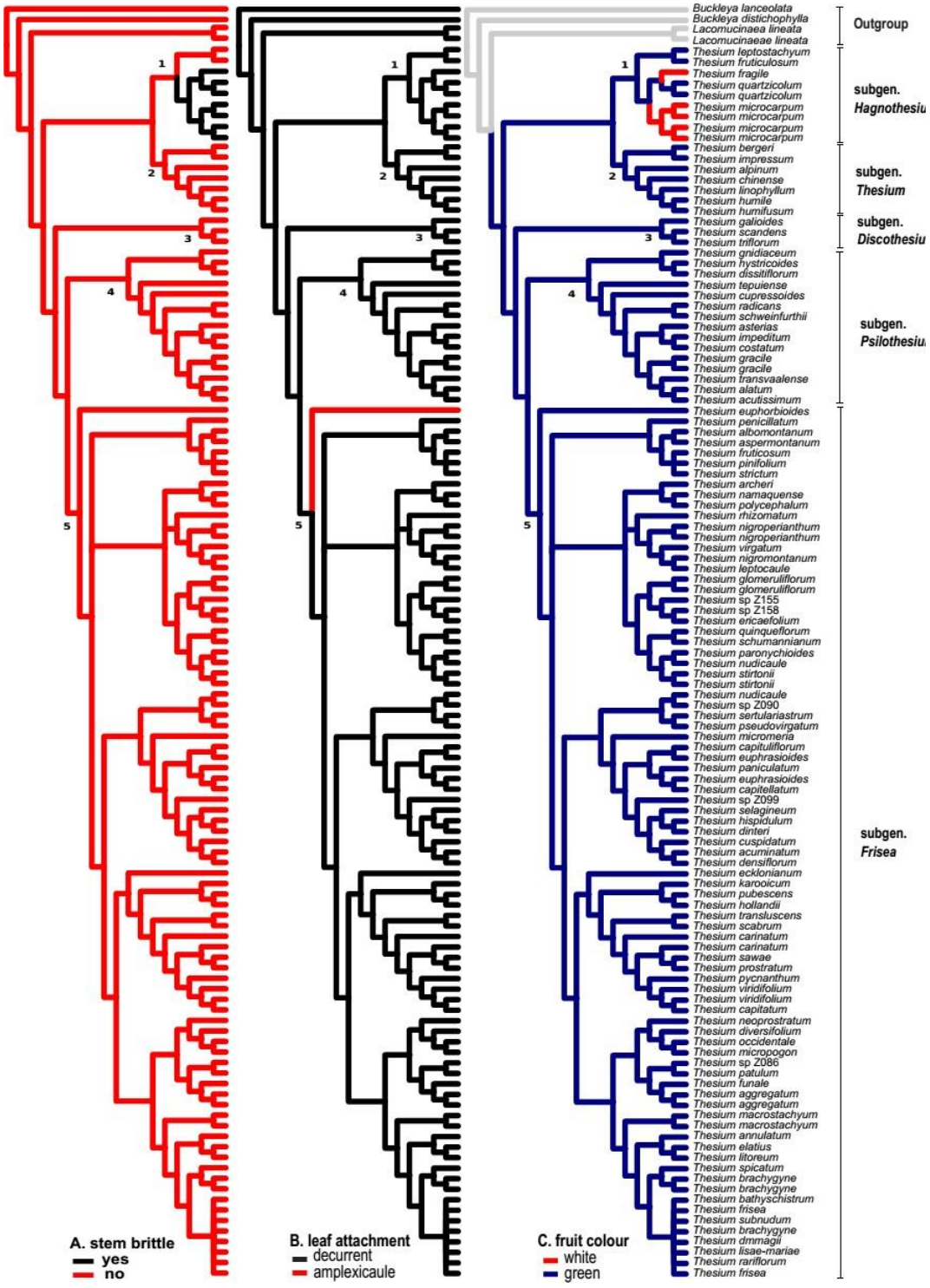



**Appendix Fig. S2.2 (A and B):** The 50% majority-rule phylogenetic tree obtained from the Bayesian analysis of 223 taxa used for the trnL-F data set. Numbers above each branch represent the percentage posterior probabilities (> 60%). Coloured leaves and taxa names show geographical range estimates of species. Numbers 1–5 and letters A–E indicate nodes discussed in the text.


Buckleya distichophylla
Thesium subsucculentum
Thesium humile
Thesium humifusum
Thesium linophyllum
Thesium humifusum
Thesium humifusum
Thesium fruticulosum
Thesium hirtum
Thesium fragile
Thesium fragile
Thesium quartzicolum
Thesium quartzicolum
Thesium quartzicolum
Thesium microcarpum
Thesium microcarpum
Thesium microcarpum
Thesium whitehillensis
Thesium galioides
Thesium scandens
Thesium triflorum
Thesium lacinulatum
Thesium dissitiflorum
Thesium gnidiaceum
Thesium acutissimum
Thesium transvaalense
Thesium racemosum
Thesium alatum
Thesium gracile
Thesium acutissimum
Thesium sp. S13474
Thesium euphorbioides
Thesium ericaefolium
Thesium spicatum
Thesium bathyschistum
Thesium spicatum
Thesium lisae-mariae
Thesium neoprostratum
Thesium elatius
Thesium micromeria
Thesium brachygyne
Thesium densiflorum
Thesium spicatum
Thesium aggregatum
Thesium micromeria
Thesium dmmagii
Thesium bathyschistum
Thesium subnudum
Thesium albomontanum
Thesium archeri
Thesium sawae
Thesium viridifolium
Thesium carinatum
Thesium cornigerum
Thesium nigromontanum
Thesium densiflorum
Thesium sp. Z082
Thesium acuminatum
Thesium elatius
Thesium ericaefolium
Thesium euphrasioides
Thesium exile
Thesium fallax
Thesium flexuosum
Thesium fruticosum
Thesium glomeratum
Thesium glomeratum
Thesium capitellatum
Thesium hillianum
Thesium annulatum
Thesium karooicum
Thesium leptocaule
Thesium litoreum
Thesium minus
Thesium sp. MM4302
Thesium nudicaule
Thesium orientale
Thesium paniculatum
Thesium prostratum
Thesium commutatum
Thesium pubescens
Thesium pubescens
Thesium pycnanthus
Thesium nigroperianthum
Thesium sonderianum
Thesium hystrix
Thesium hystricoides
Thesium carinatum
Thesium scabrum
Thesium neoprostratum
Thesium sp. Z096
Thesium nigroperianthum
Thesium nigromontanum
Outgroup
subgen. Thesium
subgen. Hagnothesium
subgen. Discothesium
subgen. Psilothesium
subgen. Frisea
Legend for the colours
Eastern Asia
North America
South Africa (SA)
subtropical Africa/SA
Europe/Western Asia
Tropical Africa
South America
Canary Islands
A
to Fig. S3B




**Appendix Fig. S2.3 (A and B):** The 50% majority-rule phylogenetic tree obtained from the Bayesian analysis of 165 taxa used for the matK data set. Numbers above each branch represent the percentage posterior probabilities (> 60%). Coloured leaves and taxa names show geographical range estimates of species. Numbers 1–5 and letters A–E indicate nodes discussed in the text.



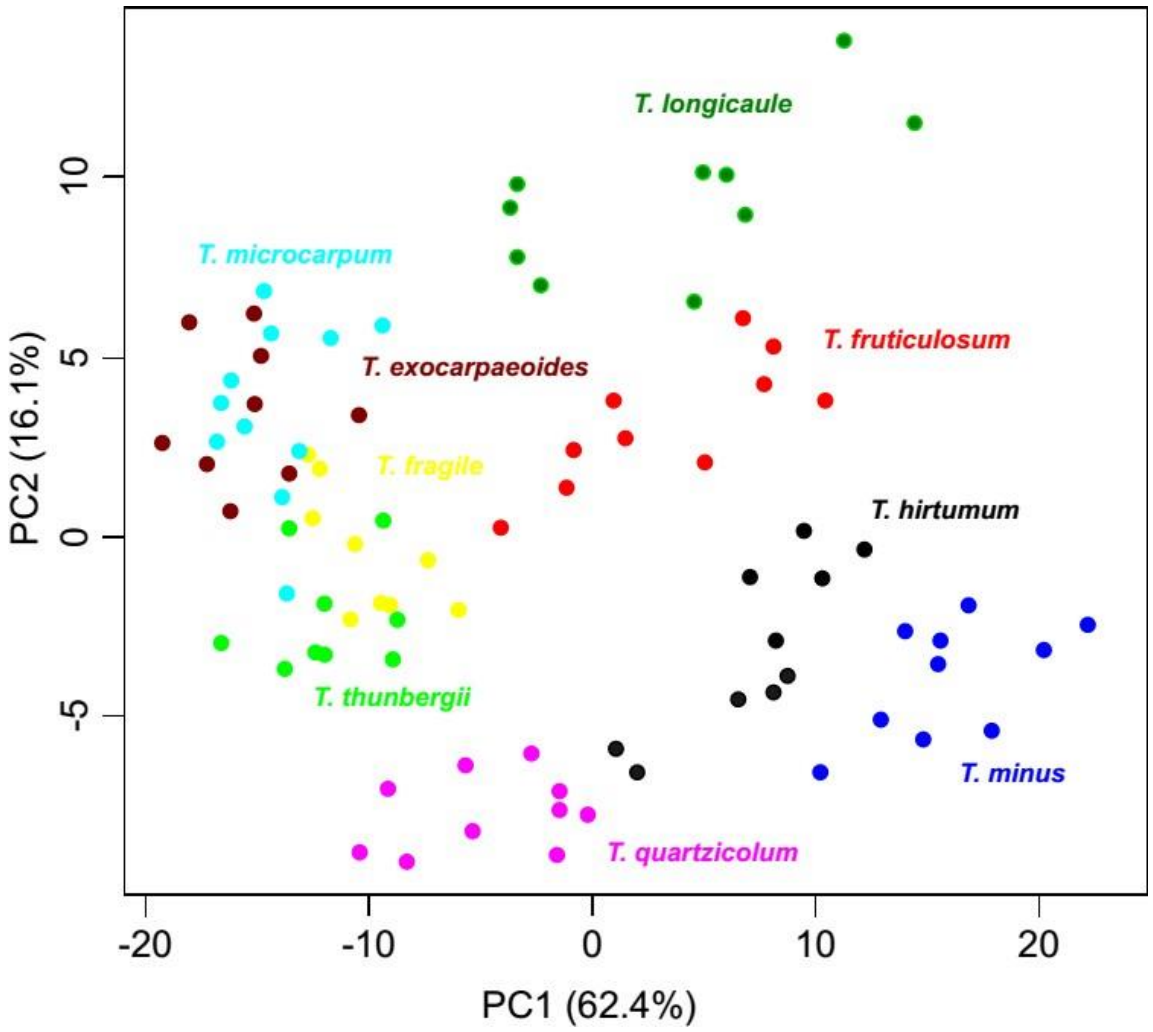

**Appendix Fig. S2.4 (A – C):** Optimized morphological traits on the combined Bayesian phylogenetic tree to estimate ancestral character evolution of representative traits in *Thesium*. The legend explains the colours used to depict the character evolutionary patterns. Grey colour of the outgroups indicates characters not studied. Numbers 1–5 indicate major clades (subgenera) discussed in the text.

**Appendix Table S3.1:** The 30 discrete and 19 continuous traits data frame of the specimens in subgenus *Hagnothesium* used for morphometric analyses. All measurements are in mm except for the plant height (cm).

| | *T. fragile* | *T. fruticulosum* | *T. hirtum* | *T. leptostachyum* | *T. longicaule* | *T. microcarpum* | *T. minus* | *T. quartzicolum* |
|---|---|---|---|---|---|---|---|---|
| Life form | perennial | perennial | perennial | annual | perennial | perennial | annual | annual |
| Growth exposure | heath–like | under shrubs | under shrubs | ? | heath–like | under shrubs | under shrubs | heath–like |
| Male and female | similar | dissimilar | dissimilar | ? | dissimilar | similar | dissimilar | similar |
| Root system | woody taproot | slender fibrous | slender fibrous | ? | slender fibrous | slender fibrous | rhizome fibrous | slender fibrous |
| Plant height (cm) | 21–40 | 18–31 | 9–25 | ? | 20–30 | 22–38 | 5–10 | 8–15 |
| Plant surface | glabrous | glabrous | scabrid | glabrous | subglabrous | glabrous | glabrous | glabrous |
| Stem diameter (mm) | 1.3–4 | 2–3.5 | 1–3 | ? | 1–3 | 0.9–3 | 0.5–1.2 | 1.3–3 |
| Stem transverse section | sulcate | sulcate | sulcate | sulcate | sulcate | terete | sulcate | terete |
| Branching pattern | virgate | fastigiate | virgate | ? | virgate | fastigiate | fastigiate | virgate |
| Number of branches | 4–10 | 5–15 | 4–12 | ? | 3–12 | 5–12 | 4–12 | 3–10 |
| Branch distribution | sparingly | dense at basal portion | dense at basal portion | ? | sparingly | dense at distal portion | dense at basal portion | sparingly |
| Male internode length (mm) | 8–12 | 0.5–4 | 0.7–1.6 | 0.5–3 | 4–10 | 2–6.5 | 2.5–8 | 3–6.5 |
| Female internode length (mm) | 2–13 | 0.5–3 | 0.7–1.5 | ? | 1–5 | 3.5–7.5 | 1.5–2.5 | 4–8 |
| Leaf shape | scale–like to absent | linear | lanceolate | lanceolate | acicular | scale–like to absent | linear | scale–like |
| Base leaf density | sparse | dense | dense | ? | dense | sparse | dense | sparse |
| Male leaf length | 1–2.4 | 3–5.3 | 2.4–6 | ? | 5–10 | 1–2 | 5.2–12.7 | 1–2 |
| Female leaf length | 1–2.2 | 5.6– 10 | 6–12.7 | ? | 8–17.93 | 0.5–1.5 | 7.5–12.8 | 1–1.5 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Male leaf breadth | 0.6–1.2 | 0.5–1.1 | 0.5–1.5 | ? | 0.4–0.8 | 0.6–1.2 | 0.5–1 | 0.5–0.8 |
| Female leaf breadth (mm) | 0.5–1.2 | 1—3 | 1–2.3 | ? | 0.5–1.5 | 0.5–1.2 | 0.2–0.9 | 0.5–0.8 |
| Leaf midrib | not raised | raised | not raised | not raised | raised | not raised | not raised | not raised |
| Leaf margin | entire or cartiliginous | entire | scabrid | entire | entire | entire | entire | cartiliginous |
| Leaf margin texture | cartiliginous | not cartilaginous | cartilaginous | ? | cartilaginous | not cartilaginous | not cartilaginous | cartilaginous |
| Bract shape | triangular | lanceolate | lanceolate | ? | lanceolate | lanceolate | lanceolate | triangular |
| Bract midrib aspect | not raised | not raised | raised | ? | not raised | not raised | raised | not raised |
| Bract length (mm) | 0.7–1.5 | 2–6.4 | 1.8–5 | ? | 5–10 | 1–1.5 | 2.5–5.3 | 0.8–3 |
| Bract breadth (mm) | 0.5–1.3 | 1–2 | 1.2–2.9 | ? | 2–2.5 | 0.4–1 | 0.5–1.2 | 0.8–2.3 |
| Bracts and bracteoles | scale–like | leaf–like | leaf–like | leaf–like | leaf–like | scale–like | leaf–like | scale–like |
| Bracteole shape | triangular | lanceolate | linear | triangular | linear | triangular | lanceolate | triangular |
| Bracteole length | 0.5–1.2 | 1.1–4.2 | 1.1–3.2 | ? | 3–4.2 | 0.6–1 | 1.5–3.2 | 0.7–2.5 |
| Bracteole breadth | 0.4–1.2 | 0.8–2 | 0.5–2.5 | ? | 0.5–2 | 0.3–1 | 0.5–1.5 | 0.5–1.6 |
| Bracteole texture | thick | thin | thick | thick | thin | thick | thin | thin |
| Bracteole midrib | raised | raised | raised | not raised | not raised | not raised | raised | not raised |
| Bracteole margin texture | entire | entire | scabrid | ? | entire | entire | entire | serrated |
| Bract/flower length | shorter than flower | longer than flower | longer than flower | longer than flower | longer than flower | shorter than flower | longer than flower | shorter than flower |
| Flower length | 0.8–2 | 1–2.5 | 0.7–2 | ? | 2–3.7 | 2.3–4 | 1–2.5 | 2.5–5 |
| Flower breadth | 0.6–2 | 0.8–1.5 | 0.8–1.8 | ? | 0.7–1.5 | 3.8–4.8 | 0.5–1.3 | 2.2–4 |
| Perianth lobe shape | triangular | triangular | lanceolate | ? | lanceolate | ovate | lanceolate | triangular |
| Perianth lobe length | 0.5–1 | 0.5–1.2 | 0.5–1.5 | ? | 0.5–1.3 | 2–2.9 | 0.6–1.4 | 2–3.1 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Perianth lobe breadth | 0.4–0.8 | 0.5–0.9 | 0.7–1.5 | ? | 0.5–0.9 | 1.8–3.4 | 0.5–0.8 | 1–2 |
| Perianth lobe tip | obtuse | acute | acute | ? | acute | acute | acute | acute |
| Fruit elaiosome | present | short to absent | ? | ? | absent | absent | present | absent |
| Fruit colour | white | green | green | ? | green | white | green | golden–green |
| Fruit shape | truncate | ovoid | ovoid | ovoid | ovoid | ovoid | ovoid | globose |
| Fruit ribs | 5–ribbed | 10–ribbed | 10–ribbed | ? | 10–ribbed | ribs absent | 10–ribbed | ribs absent |
| Fruit length (mm) | 2–3.4 | 1.5–3 | 2–3 | ? | 1.8–2.5 | 2–3.2 | 1.3–2.8 | 1.5–3 |
| Fruit diameter (mm) | 1.8–2.7 | 1.2–2.5 | 2–2.5 | ? | 1.6–2 | 1–2 | 1–3.2 | 1–2.24 |
| Persistent perianth lobe colour | orange | green | green | ? | green | ? | green | golden–green |
| Substrate | sand dune | sandstone | sandstone/deep sand | ? | sandstone | shale and sandstone | sandstone/deep sand | quartz–silcrete |




**Appendix Fig. S3.1:** Plot of the first two Principal Components retrieved from analysis of 21 continuous morphological traits of specimens of *Thesium* subgenus *Hagnothesium*. The first axis (62.4%) and the second (16.1%) account for the overall variation.

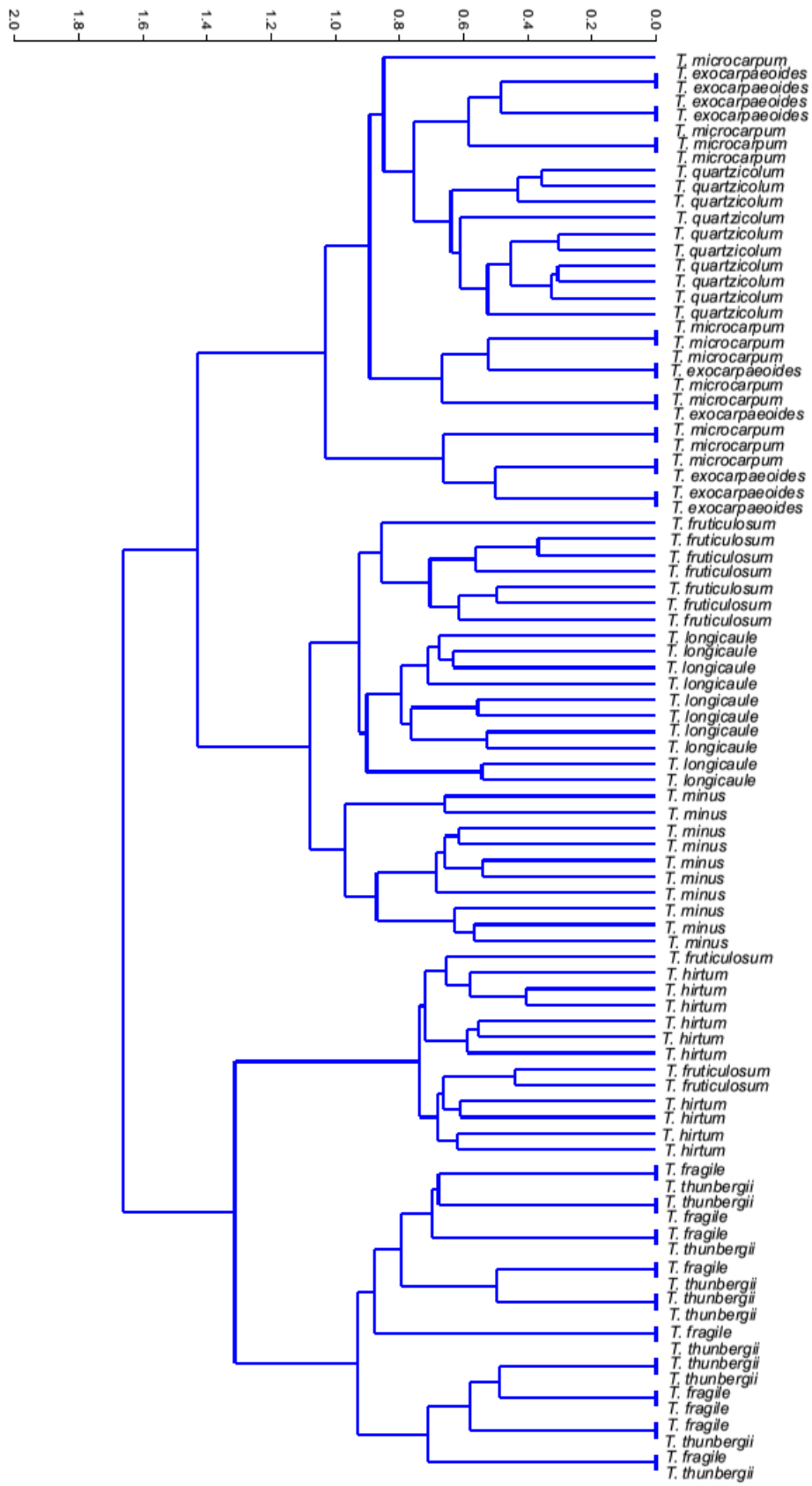



**Fig. S3.2:** A phenogram of UPGMA obtained from a cluster analysis of 19 continuous morphological traits of specimens in *Thesium* subgenus *Hagnothesium*.

**Appendix Table S3.2:** The first 10 variable PCA loadings used for species in the subgenus *Hagnothesium*.

| | PC 1 | PC 2 | PC 3 | PC 4 | PC 5 | PC 6 | PC 7 | PC 8 | PC 9 | PC 10 |
|---|---|---|---|---|---|---|---|---|---|---|
| Flower length | 0.000 | -0.053 | 0.039 | -0.05 | 0.143 | -0.016 | 0.235 | 0.169 | -0.208 | 0.116 |
| Flower breadth | 0.015 | -0.120 | 0.087 | -0.14 | -0.001 | -0.109 | 0.287 | 0.335 | -0.369 | 0.217 |
| Corolla length | 0.010 | -0.077 | 0.038 | -0.06 | 0.037 | -0.120 | 0.172 | 0.161 | -0.226 | 0.212 |
| Corolla breadth | 0.013 | -0.023 | 0.021 | -0.17 | -0.065 | 0.017 | 0.058 | 0.139 | -0.108 | 0.017 |
| Male inter node length | 0.090 | -0.201 | -0.79 | 0.806 | -0.186 | 0.404 | 0.107 | 0.141 | -0.166 | -0.006 |
| Female inter node length | 0.036 | -0.076 | 0.025 | 0.085 | 0.071 | -0.166 | 0.779 | -0.039 | 0.426 | -0.314 |
| Plant height (cm) | 0.988 | 0.102 | -0.23 | -0.30 | 0.046 | -0.079 | -0.043 | -0.022 | 0.000 | 0.033 |
| Number of branches | -0.015 | 0.358 | 0.869 | 0.316 | -0.033 | -0.088 | 0.000 | -0.049 | -0.045 | 0.036 |
| Stem diameter | 0.018 | 0.010 | -0.06 | 0.013 | -0.078 | 0.095 | 0.120 | -0.218 | 0.337 | 0.192 |
| Male leaf length | -0.091 | 0.163 | -0.28 | 0.411 | 0.591 | -0.550 | -0.104 | -0.037 | 0.001 | 0.149 |
| Female leaf length | -0.068 | 0.828 | -0.33 | -0.08 | -0.340 | 0.005 | 0.210 | 0.079 | -0.130 | 0.025 |
| Male leaf breadth | -0.009 | 0.019 | -0.08 | 0.021 | -0.034 | -0.003 | -0.081 | -0.076 | 0.099 | -0.022 |
| Female leaf breadth | -0.009 | 0.076 | -0.03 | -0.01 | -0.062 | 0.023 | -0.146 | -0.150 | 0.239 | -0.051 |
| Bract length | 0.004 | 0.150 | 0.045 | -0.08 | 0.211 | 0.177 | -0.213 | 0.795 | 0.427 | -0.132 |
| Bract breadth | 0.000 | -0.011 | 0.016 | -0.10 | -0.014 | 0.041 | 0.167 | 0.113 | 0.170 | 0.253 |
| Bracteole length | -0.002 | 0.225 | 0.022 | -0.31 | 0.636 | 0.636 | 0.165 | -0.229 | -0.152 | 0.002 |
| Bracteole breadth | -0.017 | -0.016 | -0.08 | 0.047 | -0.057 | 0.113 | 0.030 | -0.037 | 0.329 | 0.797 |
| Fruit length | 0.006 | 0.004 | -0.09 | 0.006 | -0.047 | 0.070 | -0.045 | -0.050 | 0.071 | -0.114 |
| Fruit diameter | -0.003 | 0.019 | -0.08 | 0.023 | -0.024 | 0.032 | -0.092 | -0.071 | 0.038 | 0.022 |

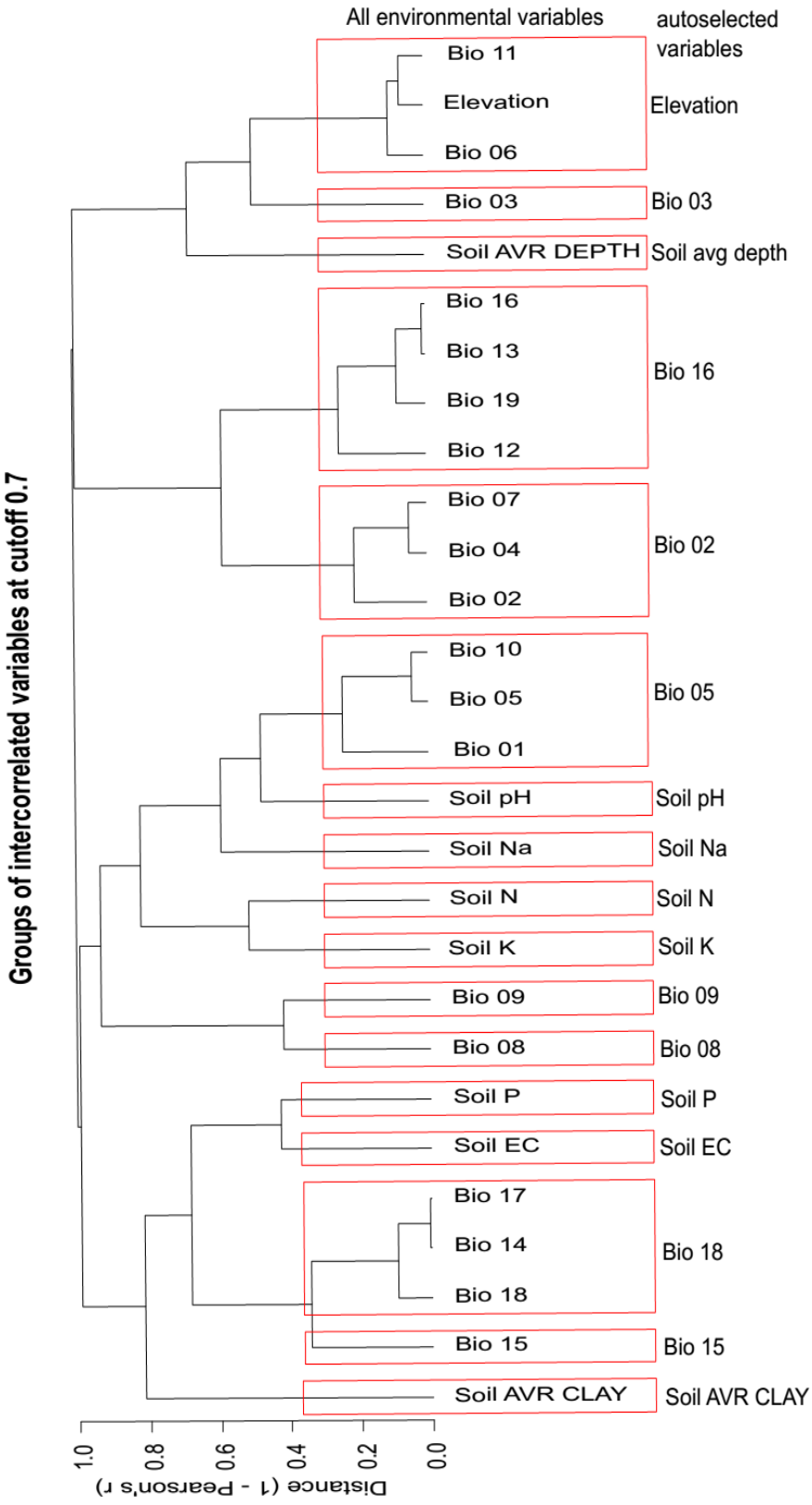
**Appendix Table S5.1:** Mean of the 14 variables used for the niche characterization of the 101 GCFR *Thesium* species

| Species | Soil depth | Soil EC | elevation | Soil K | Soil N | Soil P | Soil pH | bio02 | bio03 | bio05 | bio08 | bio09 | bio15 | bio16 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *T. acuminatum* | 570.950 | -0.970 | 301.793 | -0.772 | -1.000 | 0.182 | 4.824 | 8.589 | 52.823 | 24.045 | 12.566 | 19.225 | 62.073 | 275.345 |
| *T. aggregatum* | 569.271 | -0.909 | 383.821 | -0.664 | -0.824 | 0.129 | 5.239 | 9.985 | 53.016 | 25.388 | 12.936 | 19.091 | 53.021 | 216.821 |
| *T. albomontanum* | 264.621 | -0.875 | 1370.417 | -0.809 | -0.711 | 0.353 | 4.467 | 12.013 | 50.200 | 24.000 | 10.505 | 15.526 | 26.678 | 128.125 |
| *T. annulatum* | 409.044 | -0.906 | 1184.000 | -0.901 | -0.924 | 0.352 | 4.117 | 11.344 | 50.208 | 23.500 | 8.033 | 17.667 | 41.755 | 200.333 |
| *T. archeri* | 331.954 | -0.926 | 820.800 | -0.538 | -0.689 | 0.035 | 5.546 | 13.520 | 51.046 | 28.280 | 13.637 | 17.223 | 36.078 | 126.400 |
| *T. bathyschistum* | 460.972 | -0.857 | 315.138 | -0.723 | -0.925 | 0.209 | 5.080 | 9.312 | 53.250 | 24.569 | 12.497 | 18.987 | 48.073 | 257.759 |
| *T. brachygyne* | 341.518 | -0.873 | 713.174 | -0.867 | -0.935 | 0.261 | 4.179 | 10.790 | 52.604 | 24.648 | 10.946 | 18.222 | 51.749 | 242.913 |
| *T. capitatum* | 395.924 | -0.868 | 678.385 | -0.816 | -0.852 | 0.286 | 4.184 | 10.147 | 52.144 | 24.339 | 11.237 | 18.289 | 49.603 | 248.337 |
| *T. capitellatum* | 352.854 | -0.841 | 596.933 | -0.722 | -0.756 | 0.250 | 4.360 | 10.594 | 53.227 | 24.620 | 10.784 | 18.866 | 46.457 | 262.533 |
| *T. capituliflorum* | 454.021 | -0.892 | 488.835 | -0.777 | -0.883 | 0.212 | 4.606 | 10.352 | 52.866 | 25.042 | 11.905 | 18.985 | 51.582 | 253.200 |
| *T. carinatum* | 376.237 | -0.872 | 813.152 | -0.799 | -0.840 | 0.294 | 4.311 | 10.770 | 52.183 | 24.380 | 11.440 | 17.166 | 42.432 | 217.478 |
| *T. carinatumvar.pallidum* | 307.846 | -0.893 | 889.111 | -0.924 | -0.968 | 0.255 | 4.212 | 11.444 | 51.766 | 24.894 | 10.361 | 18.095 | 48.970 | 218.648 |
| *T. commutatum* | 432.554 | -0.873 | 413.260 | -0.731 | -0.856 | 0.266 | 4.494 | 9.095 | 52.850 | 24.035 | 12.193 | 18.330 | 51.950 | 274.313 |
| *T. densiflorum* | 414.422 | -0.858 | 549.404 | -0.792 | -0.860 | 0.281 | 4.331 | 9.849 | 51.990 | 24.550 | 11.460 | 18.624 | 52.369 | 277.192 |
| *T. disciflorum* | 281.518 | -0.930 | 824.600 | -0.689 | -0.616 | 0.118 | 4.916 | 13.258 | 52.379 | 27.240 | 13.820 | 17.160 | 32.159 | 128.600 |
| *T. dissitiflorum* | 468.574 | -0.964 | 754.667 | -0.703 | -0.675 | -0.007 | 5.094 | 13.692 | 51.941 | 28.417 | 10.978 | 19.992 | 51.285 | 126.333 |
| *T. diversifolium* | 536.314 | -0.994 | 701.200 | -0.840 | -1.049 | -0.030 | 4.338 | 11.818 | 51.406 | 26.620 | 10.897 | 20.683 | 57.279 | 156.400 |
| *T. dmmagiae* | 280.854 | -0.715 | 209.125 | -0.396 | -0.469 | 0.267 | 5.848 | 11.190 | 53.091 | 27.862 | 12.944 | 20.885 | 26.967 | 141.625 |
| *T. ecklonianum* | 802.316 | -0.975 | 137.778 | -0.715 | -1.080 | 0.051 | 5.177 | 9.737 | 53.397 | 25.767 | 13.093 | 20.500 | 59.131 | 260.333 |
| *T. elatius* | 643.759 | -0.911 | 159.143 | -0.462 | -0.538 | -0.134 | 6.823 | 12.720 | 58.813 | 28.071 | 13.754 | 21.433 | 62.146 | 101.714 |
| *T. ericaefolium* | 402.270 | -0.839 | 612.413 | -0.746 | -0.820 | 0.272 | 4.546 | 10.036 | 52.705 | 24.546 | 12.975 | 16.929 | 36.190 | 210.798 |
| *T. euphorbioides* | 395.032 | -0.851 | 477.732 | -0.724 | -0.806 | 0.268 | 4.467 | 10.138 | 53.575 | 24.697 | 11.918 | 18.905 | 43.435 | 260.408 |
| *T. euphrasioides* | 365.001 | -0.811 | 416.000 | -0.768 | -0.771 | 0.307 | 4.299 | 9.851 | 51.999 | 24.911 | 11.512 | 19.490 | 54.080 | 312.222 |
| *T. fallax* | 457.791 | -0.953 | 200.000 | -0.557 | -0.821 | 0.113 | 5.261 | 9.828 | 55.100 | 25.040 | 12.807 | 19.403 | 46.021 | 231.000 |
| *T. flexousum* | 539.651 | -0.851 | 391.208 | -0.727 | -0.687 | 0.044 | 5.560 | 11.442 | 54.624 | 27.208 | 17.148 | 15.538 | 21.121 | 154.375 |
| *T. foliosum* | 405.533 | -0.778 | 552.963 | -0.711 | -0.777 | 0.176 | 4.923 | 10.709 | 54.458 | 25.893 | 16.815 | 12.840 | 20.008 | 185.796 |
| *T. fragile* | 644.981 | -0.846 | 177.160 | -0.610 | -0.839 | 0.101 | 5.940 | 9.650 | 53.788 | 25.692 | 14.025 | 19.156 | 39.874 | 211.630 |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *T. frisea* | 672.524 | -0.905 | 168.707 | -0.563 | -0.800 | 0.070 | 5.755 | 10.220 | 52.951 | 26.389 | 13.250 | 20.682 | 54.357 | 233.653 |
| *T. friseavar.thunbergii* | 641.140 | -0.888 | 118.455 | -0.616 | -0.750 | 0.059 | 5.738 | 8.677 | 52.285 | 25.018 | 14.033 | 20.298 | 60.913 | 257.000 |
| *T. fructicosum* | 371.882 | -0.836 | 776.556 | -0.754 | -0.605 | 0.230 | 5.937 | 11.750 | 57.315 | 26.100 | 17.850 | 12.500 | 30.163 | 185.000 |
| *T. fruticulosum* | 578.200 | -0.818 | 317.599 | -0.613 | -0.736 | 0.212 | 5.050 | 9.927 | 53.423 | 25.378 | 13.328 | 19.016 | 44.709 | 243.767 |
| *T. funale* | 579.871 | -0.868 | 227.168 | -0.651 | -0.789 | 0.189 | 5.043 | 9.300 | 52.679 | 25.280 | 13.226 | 19.694 | 51.627 | 249.842 |
| *T. galioides* | 406.364 | -0.858 | 503.714 | -0.686 | -0.602 | 0.144 | 5.555 | 12.408 | 54.202 | 27.469 | 17.332 | 16.009 | 22.359 | 124.886 |
| *T. glomeratum* | 606.816 | -0.911 | 172.500 | -0.806 | -0.965 | 0.031 | 5.751 | 11.896 | 55.666 | 28.750 | 15.717 | 19.442 | 46.156 | 157.000 |
| *T. glomeruliflorum* | 443.328 | -0.748 | 546.333 | -0.747 | -0.753 | 0.231 | 4.440 | 10.673 | 54.342 | 25.450 | 15.799 | 15.927 | 20.504 | 178.167 |
| *T. gnidiaceum* | 410.971 | -0.851 | 491.071 | -0.757 | -0.733 | 0.099 | 5.633 | 11.361 | 55.811 | 26.893 | 16.567 | 15.257 | 28.968 | 188.571 |
| *T. gnidiaceumvar.zeyheri* | 502.984 | -0.822 | 481.000 | -0.684 | -0.744 | 0.227 | 4.815 | 11.912 | 54.279 | 27.050 | 16.792 | 16.617 | 19.964 | 132.000 |
| *T. helichrysioides* | 385.588 | -0.874 | 519.500 | -0.848 | -0.935 | 0.014 | 5.107 | 11.267 | 52.514 | 26.750 | 11.717 | 20.350 | 40.214 | 136.000 |
| *T. hillianum* | 246.961 | -0.941 | 790.000 | -0.346 | -0.472 | 0.033 | 6.707 | 14.458 | 52.271 | 30.150 | 14.675 | 19.458 | 35.954 | 77.500 |
| *T. hirtum* | 510.805 | -0.920 | 302.341 | -0.612 | -0.767 | 0.191 | 5.187 | 9.528 | 53.320 | 24.873 | 13.036 | 18.963 | 51.572 | 229.976 |
| *T. hispidulum* | 424.017 | -0.960 | 533.229 | -0.797 | -0.862 | 0.087 | 4.931 | 12.514 | 52.135 | 27.815 | 11.469 | 21.486 | 58.301 | 182.354 |
| *T. hollandii* | 561.616 | -0.808 | 358.667 | -0.769 | -0.802 | 0.042 | 5.671 | 11.044 | 53.914 | 27.067 | 18.050 | 13.183 | 16.288 | 163.167 |
| *T. imbricatum* | 485.818 | -0.873 | 767.222 | -0.806 | -0.855 | 0.115 | 5.085 | 11.778 | 52.021 | 25.744 | 11.885 | 17.570 | 39.680 | 170.444 |
| *T. impeditum* | 645.432 | -0.689 | 199.333 | -0.526 | -0.650 | 0.217 | 5.119 | 10.950 | 54.514 | 26.567 | 12.900 | 20.567 | 36.796 | 250.000 |
| *T. junceum* | 483.373 | -0.818 | 419.906 | -0.706 | -0.732 | 0.137 | 5.653 | 10.993 | 55.471 | 26.678 | 16.859 | 14.826 | 25.249 | 185.625 |
| *T, juncifolium* | 519.009 | -0.928 | 522.744 | -0.801 | -0.827 | 0.127 | 4.793 | 11.734 | 51.816 | 26.958 | 11.778 | 20.516 | 51.788 | 202.605 |
| *T. karooicum* | 318.677 | -0.879 | 821.556 | -0.639 | -0.521 | 0.155 | 5.561 | 13.091 | 52.176 | 27.656 | 15.791 | 16.109 | 25.070 | 101.111 |
| *T. leptocaule* | 508.147 | -0.859 | 337.600 | -0.704 | -0.798 | 0.055 | 5.597 | 10.838 | 54.797 | 26.672 | 16.579 | 15.621 | 23.030 | 163.840 |
| *T. leptostachyum* | 311.838 | -0.846 | 558.500 | -0.666 | -0.642 | 0.213 | 5.199 | 12.013 | 56.715 | 26.800 | 14.367 | 17.267 | 37.615 | 210.500 |
| *T. lisae-mariae* | 354.558 | -0.850 | 357.750 | -0.735 | -0.758 | 0.081 | 5.792 | 11.554 | 58.515 | 26.825 | 17.067 | 15.033 | 27.078 | 157.000 |
| *T. litoreum* | 881.969 | -0.838 | 290.667 | -0.667 | -0.757 | 0.091 | 5.199 | 9.075 | 51.982 | 24.856 | 12.559 | 19.917 | 63.270 | 268.333 |
| *T. longicaule* | 606.435 | -0.866 | 366.333 | -0.625 | -0.839 | 0.178 | 5.424 | 9.598 | 53.248 | 25.133 | 14.185 | 17.220 | 46.779 | 247.000 |
| *T. macrostachyum* | 593.341 | -0.939 | 445.438 | -0.714 | -0.820 | 0.074 | 5.038 | 11.710 | 52.168 | 27.188 | 11.610 | 21.164 | 55.813 | 198.375 |
| *T. microcarpum* | 552.922 | -0.845 | 456.272 | -0.662 | -0.650 | 0.115 | 5.564 | 11.227 | 53.948 | 26.611 | 15.348 | 16.955 | 28.211 | 161.767 |
| *T. micromeria* | 528.978 | -0.903 | 121.200 | -0.663 | -0.743 | 0.144 | 5.507 | 10.870 | 52.844 | 27.340 | 12.857 | 21.543 | 49.876 | 259.200 |
| *T. micropogon* | 460.870 | -0.876 | 476.000 | -0.845 | -0.932 | 0.174 | 4.958 | 11.092 | 54.992 | 25.883 | 13.811 | 18.506 | 34.604 | 211.833 |
| *T. minus* | 477.573 | -0.850 | 404.056 | -0.608 | -0.699 | 0.249 | 5.077 | 10.502 | 53.837 | 25.628 | 13.773 | 17.675 | 41.243 | 252.833 |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *T. namaquense* | 388.185 | -0.962 | 829.647 | -0.505 | -0.450 | 0.064 | 6.156 | 14.274 | 54.415 | 28.900 | 13.160 | 19.076 | 36.011 | 82.588 |
| *T. nigromantanum* | 440.952 | -0.861 | 533.836 | -0.786 | -0.849 | 0.195 | 4.852 | 10.667 | 53.514 | 25.529 | 14.211 | 16.921 | 35.356 | 205.795 |
| *T. nudicaule* | 511.650 | -0.900 | 610.771 | -0.730 | -0.746 | 0.142 | 5.292 | 11.891 | 53.645 | 26.451 | 12.509 | 18.189 | 44.732 | 174.743 |
| *T. occidentale* | 350.420 | -0.967 | 781.500 | -0.684 | -0.642 | 0.127 | 5.264 | 12.633 | 53.188 | 27.500 | 12.760 | 19.754 | 40.171 | 115.375 |
| *T. paniculatum* | 421.439 | -0.755 | 593.459 | -0.743 | -0.698 | 0.384 | 4.027 | 8.975 | 51.735 | 23.422 | 10.902 | 18.336 | 55.670 | 316.243 |
| *T. paronychioides* | 541.576 | -0.861 | 327.167 | -0.739 | -0.892 | -0.005 | 6.122 | 11.328 | 54.910 | 27.733 | 18.219 | 15.303 | 18.765 | 157.667 |
| *T. patulum* | 626.777 | -0.913 | 174.162 | -0.536 | -0.690 | 0.037 | 6.060 | 11.199 | 52.705 | 27.649 | 13.098 | 21.455 | 53.193 | 206.189 |
| *T. penicillatum* | 364.063 | -0.746 | 698.907 | -0.742 | -0.762 | 0.335 | 4.280 | 9.882 | 52.689 | 24.042 | 13.021 | 15.671 | 33.830 | 239.326 |
| *T. pinifolium* | 300.191 | -0.779 | 920.571 | -0.867 | -0.825 | 0.445 | 3.753 | 10.087 | 51.656 | 23.371 | 10.471 | 17.085 | 44.979 | 266.810 |
| *T. polycephalum* | 390.028 | -1.127 | 271.333 | -0.323 | -0.635 | -0.121 | 6.176 | 13.447 | 55.628 | 28.867 | 13.067 | 22.272 | 62.709 | 154.000 |
| *T. prostratum* | 351.019 | -0.964 | 981.600 | -0.996 | -1.049 | 0.092 | 4.048 | 12.515 | 51.194 | 25.820 | 9.120 | 19.543 | 51.631 | 154.600 |
| *T. pseudovirgatum* | 382.455 | -0.902 | 446.174 | -0.821 | -0.937 | 0.264 | 4.303 | 9.309 | 52.447 | 24.213 | 11.614 | 19.017 | 58.963 | 289.435 |
| *T. pubescens* | 704.051 | -1.009 | 288.333 | -0.593 | -0.860 | -0.049 | 5.662 | 11.287 | 53.279 | 27.103 | 12.912 | 21.015 | 61.436 | 192.538 |
| *T. pycnanthum* | 309.587 | -0.873 | 766.750 | -0.856 | -0.893 | 0.260 | 4.529 | 11.169 | 51.688 | 24.979 | 10.444 | 18.461 | 44.273 | 239.208 |
| *T. quartzicolum* | 349.178 | -0.751 | 281.692 | -0.550 | -0.582 | 0.211 | 5.695 | 11.144 | 52.966 | 27.469 | 13.003 | 20.723 | 27.226 | 139.308 |
| *T. quinqueflorum* | 350.069 | -0.843 | 460.615 | -0.692 | -0.793 | 0.331 | 4.147 | 9.573 | 53.577 | 24.000 | 11.691 | 18.221 | 46.400 | 281.077 |
| *T. rariflorum* | 493.103 | -0.900 | 249.429 | -0.663 | -0.913 | 0.223 | 5.200 | 10.429 | 53.608 | 25.929 | 12.545 | 20.488 | 54.455 | 247.857 |
| *T. rhizomatum* | 318.231 | -0.760 | 206.000 | -0.629 | -0.655 | 0.216 | 5.715 | 11.845 | 53.324 | 28.380 | 13.397 | 21.583 | 27.773 | 139.800 |
| *T. rufescens* | 356.087 | -0.838 | 104.250 | -0.602 | -0.768 | 0.006 | 6.285 | 10.548 | 54.060 | 27.275 | 14.733 | 20.992 | 28.473 | 143.500 |
| *T. sawae* | 268.685 | -0.822 | 574.000 | -0.977 | -1.183 | 0.210 | 4.762 | 10.638 | 52.789 | 25.350 | 11.158 | 19.192 | 40.927 | 202.500 |
| *T. scabrum* | 461.664 | -0.849 | 486.742 | -0.736 | -0.751 | 0.264 | 4.444 | 9.980 | 52.170 | 24.842 | 11.488 | 19.152 | 54.055 | 288.636 |
| *T. scandens* | 517.684 | -0.841 | 310.273 | -0.825 | -0.572 | -0.029 | 5.893 | 11.644 | 55.244 | 27.809 | 19.174 | 14.418 | 18.462 | 141.818 |
| *T. schumannianum* | 661.185 | -0.782 | 282.714 | -0.644 | -0.675 | 0.279 | 4.644 | 8.098 | 51.503 | 23.829 | 12.369 | 19.226 | 61.487 | 293.286 |
| *T. scirpioides* | 405.692 | -0.932 | 433.000 | -0.848 | -1.122 | 0.066 | 5.086 | 12.583 | 51.152 | 28.200 | 11.350 | 21.867 | 57.380 | 218.000 |
| *T. sedifolium* | 472.564 | -0.818 | 546.545 | -0.743 | -0.849 | 0.303 | 4.150 | 9.147 | 53.030 | 23.536 | 11.480 | 18.402 | 46.273 | 275.136 |
| *T. selagineum* | 436.801 | -0.977 | 801.000 | -0.809 | -0.885 | 0.105 | 4.870 | 13.089 | 52.915 | 27.000 | 10.478 | 20.561 | 51.715 | 151.000 |
| *T. sertulariastrum* | 378.534 | -0.827 | 371.667 | -0.581 | -0.684 | 0.091 | 5.204 | 11.144 | 54.626 | 26.711 | 14.548 | 16.922 | 27.978 | 166.222 |
| *T. spicatum* | 407.623 | -0.851 | 443.420 | -0.772 | -0.879 | 0.254 | 4.548 | 9.565 | 52.593 | 24.553 | 11.989 | 18.928 | 52.169 | 265.148 |
| *T. spinosum* | 674.965 | -0.958 | 296.950 | -0.557 | -0.614 | -0.089 | 6.090 | 11.725 | 56.758 | 27.140 | 13.827 | 20.685 | 59.058 | 127.050 |
| *T. spinulosum* | 370.626 | -0.878 | 662.621 | -0.810 | -0.925 | 0.278 | 4.337 | 10.242 | 52.954 | 24.234 | 10.971 | 18.406 | 47.521 | 243.310 |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *T. squarrosum* | 425.892 | -0.784 | 541.615 | -0.719 | -0.625 | 0.200 | 5.742 | 11.087 | 57.087 | 26.254 | 17.217 | 13.754 | 25.204 | 197.231 |
| *T. stirtonii* | 427.435 | -0.741 | 221.600 | -0.493 | -0.613 | 0.356 | 5.572 | 10.498 | 53.518 | 26.480 | 12.663 | 20.207 | 34.743 | 186.600 |
| *T. strictum* | 416.033 | -0.888 | 497.524 | -0.737 | -0.747 | 0.160 | 4.823 | 11.113 | 53.086 | 26.265 | 13.466 | 18.556 | 44.474 | 212.853 |
| *T. subnudum* | 428.778 | -0.865 | 591.550 | -0.779 | -0.802 | 0.197 | 4.921 | 11.296 | 53.259 | 26.105 | 13.904 | 17.239 | 35.572 | 187.488 |
| *T. susannae* | 300.525 | -0.808 | 695.857 | -0.784 | -0.760 | 0.262 | 3.880 | 11.563 | 55.190 | 25.729 | 16.405 | 15.114 | 17.239 | 128.143 |
| *T. translucens* | 305.100 | -0.854 | 621.619 | -0.816 | -0.887 | 0.274 | 4.241 | 10.420 | 52.786 | 24.571 | 11.156 | 18.983 | 43.983 | 228.476 |
| *T. triflorum* | 752.847 | -0.825 | 119.500 | -0.921 | -0.637 | -0.044 | 6.284 | 11.864 | 56.891 | 28.550 | 18.296 | 16.894 | 18.716 | 165.375 |
| *T. umbelliferum* | 474.366 | -0.832 | 784.333 | -0.774 | -0.803 | 0.335 | 4.750 | 10.932 | 53.839 | 24.533 | 14.606 | 14.125 | 30.041 | 176.667 |
| *T. urceolatum* | 408.234 | -0.995 | 563.214 | -0.523 | -0.477 | -0.068 | 5.861 | 13.333 | 55.807 | 28.693 | 13.213 | 21.144 | 51.928 | 103.714 |
| *T. virgatum* | 460.871 | -0.871 | 503.064 | -0.765 | -0.837 | 0.174 | 4.724 | 10.584 | 53.036 | 25.587 | 13.046 | 18.255 | 43.660 | 217.284 |
| *T. viridifolium* | 558.923 | -0.941 | 197.556 | -0.716 | -0.921 | 0.175 | 4.820 | 8.048 | 53.023 | 23.794 | 13.009 | 19.090 | 62.273 | 274.944 |
| *T. whitehillensis* | 496.269 | -0.886 | 648.400 | -0.415 | -0.514 | 0.030 | 6.532 | 12.962 | 51.867 | 28.760 | 13.837 | 17.270 | 27.384 | 99.600 |




**Appendix Fig. S5.1:** The 28 *a priori* environmental variables used for the multicollinearity test. At the tips are the 14 selected variables used for the species distribution modelling**.**

**Appendix Table S5.2:** Standard deviations of the means of environmental variables standardized for the principal component analysis (PCA).

| Species | Soil depth | Soil EC | elevation | Soil K | Soil N | Soil P | Soil pH | bio02 | bio03 | bio05 | bio08 | bio09 | bio15 | bio16 | convhull.area | max.distance | Comp.1 | Comp.2 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *T. acuminatum* | 230.795 | 0.10868 | 346.557 | 0.15295 | 0.16279 | 0.1442 | 0.89344 | 1.23713 | 0.83881 | 1.16759 | 1.67678 | 1.13852 | 7.19397 | 38.8663 | 8.49E+09 | 191025 | -1.9029 | 0.81975 |
| *T. aggregatum* | 292.097 | 0.12118 | 440.137 | 0.22367 | 0.27605 | 0.25363 | 1.14643 | 1.99215 | 2.25221 | 2.28025 | 2.12055 | 3.44059 | 17.2997 | 64.4761 | 1.34E+11 | 666339 | 2.62576 | 0.63071 |
| *T. albomontanum* | 107.681 | 0.05628 | 514.248 | 0.21242 | 0.23689 | 0.22519 | 1.02287 | 1.33208 | 1.91313 | 3.86737 | 4.98399 | 4.55004 | 10.248 | 37.3937 | 9.227E+09 | 191512 | 1.44694 | -3.2935 |
| *T. annulatum* | 326.132 | 0.06685 | 837.211 | 0.09144 | 0.12685 | 0.31069 | 0.69742 | 1.6231 | 3.75745 | 5.08626 | 3.65061 | 4.24974 | 16.6022 | 41.3078 | 1860.7674 | 943.761 | 3.76285 | -3.6608 |
| *T. archeri* | 82.7838 | 0.02954 | 320.552 | 0.25666 | 0.33712 | 0.1461 | 1.15235 | 1.12519 | 0.96499 | 1.7427 | 5.14208 | 3.33101 | 14.236 | 99.984 | 3.942E+09 | 174321 | 0.62086 | -1.7616 |
| *T. bathyschistum* | 243.182 | 0.10096 | 348.025 | 0.23455 | 0.22235 | 0.20575 | 1.17298 | 1.46064 | 2.0128 | 1.71133 | 1.77102 | 2.21813 | 11.7033 | 73.4451 | 3.181E+10 | 292854 | 0.71857 | 0.78717 |
| *T. brachygyne* | 201.153 | 0.09021 | 428.073 | 0.23649 | 0.30239 | 0.22012 | 0.68788 | 1.67941 | 1.98081 | 1.88556 | 2.28421 | 3.25462 | 13.3889 | 80.987 | 4.189E+10 | 359941 | 1.22219 | 0.14388 |
| *T. capitatum* | 196.37 | 0.10857 | 449.125 | 0.18794 | 0.23776 | 0.1923 | 0.66524 | 1.59121 | 1.93997 | 2.05981 | 2.54789 | 2.85144 | 14.1813 | 84.7011 | 1.02E+11 | 674881 | 1.02229 | -0.2512 |
| *T. capitellatum* | 129.13 | 0.10106 | 469.057 | 0.20381 | 0.16968 | 0.16899 | 0.98543 | 1.58659 | 1.65056 | 2.72166 | 2.04102 | 2.24877 | 9.72756 | 76.802 | 1.301E+10 | 218894 | 0.41967 | -0.5635 |
| *T. capituliflorum* | 285.327 | 0.09963 | 432.269 | 0.2234 | 0.243 | 0.20206 | 0.98572 | 1.72656 | 2.23692 | 1.90971 | 1.83625 | 2.98498 | 13.1949 | 81.7582 | 9.583E+10 | 579592 | 1.48918 | 0.51744 |
| *T. carinatum* | 187.408 | 0.09288 | 579.857 | 0.21538 | 0.21374 | 0.20763 | 0.7906 | 1.49655 | 2.18268 | 2.67895 | 3.12635 | 4.5776 | 15.6505 | 94.5306 | 9.92E+10 | 543284 | 2.1325 | -1.7563 |
| *T. sawae* | 168.765 | 0.0997 | 483.685 | 0.19336 | 0.27254 | 0.22546 | 0.67561 | 1.37315 | 1.37537 | 2.74085 | 2.59607 | 3.9657 | 12.7948 | 84.2371 | 6.925E+10 | 448315 | 1.19328 | -0.8799 |
| *T. commutatum* | 209.565 | 0.1143 | 332.411 | 0.1263 | 0.20598 | 0.17651 | 0.82509 | 1.58364 | 1.48728 | 1.4741 | 2.06858 | 2.02002 | 12.7759 | 61.9767 | 7.107E+10 | 634790 | -0.2996 | 0.51429 |
| *T. densiflorum* | 239.368 | 0.11353 | 406.198 | 0.18764 | 0.21596 | 0.17306 | 0.73808 | 1.66151 | 1.54504 | 2.17774 | 2.28578 | 2.56641 | 13.205 | 74.7495 | 7.498E+10 | 511256 | 0.66516 | 0.18809 |
| *T. disciflorum* | 76.9704 | 0.0364 | 286.234 | 0.14871 | 0.27828 | 0.12092 | 0.94742 | 1.3311 | 1.07474 | 1.7358 | 4.55379 | 4.50411 | 16.9154 | 75.225 | 2.726E+10 | 255709 | -0.0926 | -2.304 |
| *T. dissitiflorum* | 297.649 | 0.10154 | 412.606 | 0.14618 | 0.18901 | 0.12591 | 0.79232 | 0.69446 | 1.65917 | 1.74174 | 1.64187 | 4.08584 | 14.8527 | 52.0794 | 1.08E+10 | 187029 | -0.611 | -0.6738 |
| *T. diversifolium* | 60.2135 | 0.05556 | 352.27 | 0.26955 | 0.20696 | 0.0476 | 0.90248 | 0.75481 | 0.68427 | 1.10995 | 1.65548 | 1.02781 | 6.98832 | 47.8884 | 1.007E+09 | 156148 | -3.0983 | -0.2062 |
| *T. dmmagiae* | 10.8974 | 0.00728 | 34.2321 | 0.04313 | 0.04205 | 0.04927 | 0.21975 | 0.20445 | 0.35666 | 0.0744 | 0.16231 | 0.09777 | 0.35652 | 1.40789 | 7307041.8 | 8423.43 | -8.0364 | -0.2443 |
| *T. ecklonianum* | 423.563 | 0.1043 | 226.479 | 0.28546 | 0.34366 | 0.2056 | 0.8525 | 0.84395 | 1.76453 | 0.89722 | 1.32799 | 1.0916 | 13.6917 | 53.7006 | 2.147E+09 | 168435 | -0.0436 | 2.72788 |
| *T. elatius* | 278.845 | 0.22122 | 213.44 | 0.17166 | 0.21789 | 0.23304 | 1.15187 | 1.891 | 3.79378 | 1.96116 | 1.06065 | 1.39689 | 9.48073 | 49.6479 | 5.196E+10 | 583137 | 1.64017 | 2.59621 |
| *T. ericaefolium* | 162.844 | 0.11367 | 515.508 | 0.17283 | 0.21208 | 0.19934 | 0.96521 | 1.57809 | 1.99375 | 1.88375 | 3.11013 | 3.92542 | 15.6633 | 80.5037 | 8.741E+10 | 572342 | 1.46991 | -1.1315 |
| *T. euphorbioides* | 198.772 | 0.07554 | 398.621 | 0.19941 | 0.20074 | 0.17344 | 0.94244 | 1.34638 | 1.78388 | 2.00691 | 2.52645 | 1.93734 | 13.8135 | 82.6683 | 4.625E+10 | 572411 | 0.38891 | -0.3242 |
| *T. euphrasioides* | 240.936 | 0.06843 | 296.945 | 0.19956 | 0.23227 | 0.1492 | 0.7037 | 1.20745 | 0.95706 | 1.70505 | 1.57849 | 1.50087 | 8.83465 | 62.288 | 1.313E+10 | 201945 | -1.3386 | 0.74413 |
| *T. fallax* | 276.928 | 0.04666 | 145.341 | 0.14553 | 0.07432 | 0.06612 | 0.87854 | 1.55488 | 1.93452 | 1.1149 | 1.04547 | 0.51699 | 14.9913 | 76.397 | 796599168 | 163389 | -1.7108 | 0.88087 |
| *T. flexousum* | 278.656 | 0.08532 | 406.106 | 0.17603 | 0.2036 | 0.22649 | 0.91687 | 1.14349 | 2.18345 | 1.89735 | 2.29177 | 4.63553 | 11.1236 | 35.3858 | 4.474E+10 | 658368 | 0.24859 | -0.8313 |
| *T. foliosum* | 153.546 | 0.10872 | 311.498 | 0.12412 | 0.17833 | 0.18704 | 0.80223 | 0.98018 | 2.09854 | 1.17198 | 1.57092 | 1.98049 | 6.49934 | 38.7831 | 3.037E+10 | 695748 | -1.7454 | 0.16739 |
| *T. fragile* | 341.465 | 0.12286 | 236.763 | 0.21714 | 0.19399 | 0.19342 | 1.20455 | 1.62829 | 2.24326 | 1.66572 | 2.07965 | 2.79062 | 18.6627 | 73.4394 | 1.13E+11 | 632823 | 1.55563 | 1.12236 |

| | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *T. frisea* | 306.424 | 0.12948 | 221.819 | 0.23156 | 0.27712 | 0.22484 | 0.89986 | 1.79731 | 1.85338 | 1.86914 | 1.611 | 1.83463 | 16.1933 | 60.6395 | 7.271E+10 | 486013 | 1.15215 | 2.03386 |
| *T. friseavar.thunbergii* | 341.671 | 0.12762 | 189.824 | 0.10415 | 0.35176 | 0.21669 | 0.85346 | 1.39321 | 1.11244 | 1.74059 | 1.93778 | 1.255 | 15.5655 | 46.7675 | 7.286E+09 | 266507 | 0.16074 | 2.11756 |
| *T. fruticosum* | 177.654 | 0.03626 | 292.968 | 0.12842 | 0.19953 | 0.13313 | 1.09215 | 0.3235 | 2.31084 | 1.48661 | 1.40621 | 1.75462 | 7.18724 | 48.3322 | 7.876E+09 | 466120 | -2.2626 | -0.6652 |
| *T. fruticulosum* | 326.307 | 0.11309 | 280.813 | 0.19371 | 0.18023 | 0.15622 | 1.09705 | 1.94218 | 2.0011 | 2.15262 | 2.254 | 2.88393 | 17.075 | 79.26 | 2.23E+11 | 978318 | 1.52599 | 0.65389 |
| *T. funale* | 277.952 | 0.12081 | 180.4 | 0.19106 | 0.25783 | 0.14717 | 0.89003 | 1.6395 | 1.68186 | 1.78621 | 1.55599 | 1.79752 | 18.17 | 65.5134 | 5.987E+10 | 650394 | 0.38104 | 1.60181 |
| *T. galioides* | 174.496 | 0.06987 | 299.568 | 0.1629 | 0.19586 | 0.12075 | 1.12223 | 1.21551 | 1.43984 | 1.69285 | 2.73645 | 5.07229 | 9.74065 | 53.917 | 3.237E+10 | 481893 | -0.7072 | -1.4088 |
| *T. glomeratum* | 233.841 | 0.1439 | 102.53 | 0.39795 | 0.23023 | 0.03788 | 1.37404 | 2.06829 | 4.63845 | 3.3234 | 2.80486 | 6.91786 | 29.1783 | 62.2254 | 5710.8274 | 1168.66 | 4.10352 | -0.8933 |
| *T. glomeruliflorum* | 259.502 | 0.15076 | 306.505 | 0.16449 | 0.16721 | 0.16443 | 0.85878 | 1.18817 | 2.1715 | 1.14929 | 1.69049 | 4.35768 | 9.88549 | 65.7681 | 1.368E+10 | 503261 | -0.1512 | 0.29591 |
| *T. gnidiaceum* | 176.909 | 0.07488 | 346.867 | 0.16398 | 0.20778 | 0.21631 | 1.06619 | 1.08116 | 2.20435 | 1.52642 | 3.68968 | 2.85794 | 13.5001 | 38.7293 | 8.959E+10 | 768423 | -0.0226 | -1.148 |
| *T. gnidiaceumvar.zeyheri* | 20.7138 | 0.01078 | 492.146 | 0.16883 | 0.00677 | 0.04328 | 0.49717 | 0.12374 | 0.66023 | 2.19203 | 1.16673 | 8.22601 | 3.91157 | 28.2843 | 5710.8274 | 1568.68 | -4.147 | -4.7443 |
| *T. helichrysioides* | 117.747 | 0.11586 | 560.736 | 0.08749 | 0.17177 | 0.07823 | 1.80221 | 0.83674 | 1.98035 | 0.91924 | 2.28631 | 0.2357 | 18.7533 | 4.24264 | 4860.7674 | 1143.76 | -1.1877 | -0.7811 |
| *T. hillianum* | 24.149 | 0.05152 | 96.1665 | 0.00576 | 0.12675 | 0.15514 | 0.83418 | 1.03709 | 3.08241 | 0.91924 | 4.20729 | 5.33866 | 13.0245 | 14.8492 | 2764.2736 | 7168.66 | -2.0074 | -3.1151 |
| *T. hirtum* | 214.393 | 0.10953 | 453.27 | 0.23896 | 0.19436 | 0.21415 | 1.2919 | 1.88478 | 1.92775 | 2.62574 | 0.67643 | 3.98891 | 16.1797 | 60.5601 | 3.478E+10 | 291127 | 1.67844 | 0.20596 |
| *T. hispidulum* | 194.225 | 0.07462 | 363.678 | 0.21691 | 0.24748 | 0.15652 | 0.89694 | 1.02373 | 1.17887 | 2.07662 | 1.62664 | 1.90251 | 7.76003 | 49.268 | 2.35E+10 | 240147 | -1.1288 | 0.19046 |
| *T. hollandii* | 189.014 | 0.05691 | 289.665 | 0.14928 | 0.29829 | 0.22327 | 0.91678 | 1.1385 | 0.57305 | 0.89815 | 1.22388 | 1.90146 | 0.81458 | 31.7075 | 2.685E+09 | 291570 | -2.4663 | 1.08737 |
| *T. imbricatum* | 345.904 | 0.07549 | 578.05 | 0.1814 | 0.27861 | 0.22094 | 1.42256 | 2.29515 | 1.60724 | 1.59068 | 4.09051 | 3.15819 | 17.8759 | 72.5967 | 7.65E+10 | 641999 | 2.92069 | -0.3185 |
| *T. impeditum* | 402.832 | 0.11908 | 160.004 | 0.20261 | 0.20067 | 0.13492 | 0.70612 | 1.26713 | 0.47682 | 0.11547 | 2.05149 | 0.1732 | 18.4201 | 73.9932 | 4.268E+10 | 723529 | -1.0245 | 2.69287 |
| *T. junceum* | 223.736 | 0.11056 | 278.735 | 0.16436 | 0.22034 | 0.13723 | 1.011 | 1.50107 | 2.6312 | 1.63228 | 1.89142 | 3.69059 | 12.9503 | 50.4392 | 1.19E+11 | 786779 | 0.14157 | 0.00172 |
| *T. juncifolium* | 262.758 | 0.07218 | 402.645 | 0.21923 | 0.19459 | 0.17062 | 0.91793 | 1.14945 | 1.50628 | 2.06423 | 1.90553 | 2.83805 | 15.6384 | 73.2046 | 1.25E+11 | 742286 | 0.27851 | -0.2534 |
| *T. karooicum* | 150.473 | 0.05239 | 411.624 | 0.2191 | 0.21311 | 0.16634 | 1.22366 | 0.51258 | 2.38924 | 2.01067 | 4.78612 | 4.07284 | 9.67355 | 28.1711 | 1.628E+10 | 360167 | -0.264 | -2.8139 |
| *T. leptocaule* | 279.483 | 0.09075 | 332.42 | 0.16455 | 0.27052 | 0.16525 | 1.06195 | 1.51993 | 1.97436 | 1.32619 | 2.09467 | 3.95678 | 13.9663 | 44.1368 | 6.023E+10 | 671120 | 0.2703 | 0.14929 |
| *T. leptostachyum* | 31.9412 | 0.05791 | 156.462 | 0.01444 | 0.18955 | 0.03359 | 1.20446 | 0.38971 | 2.94293 | 0.46188 | 3.11769 | 4.33013 | 2.23254 | 24.8261 | 6610.8274 | 6868.66 | -3.5865 | -2.436 |
| *T. lisae-mariae* | 47.892 | 0.16064 | 348.641 | 0.18543 | 0.23246 | 0.17817 | 0.65555 | 1.87155 | 1.88416 | 0.85 | 2.34754 | 3.56285 | 10.2704 | 54.8027 | 2.023E+10 | 524795 | -0.2856 | 0.2215 |
| *T. litoreum* | 384.773 | 0.18236 | 316.861 | 0.21355 | 0.17852 | 0.29168 | 1.46258 | 1.94079 | 1.2647 | 2.40006 | 1.35 | 1.7648 | 5.20778 | 60.3366 | 5.024E+09 | 209407 | 1.66156 | 2.63822 |
| *T.scirpioides* | 356.833 | 0.12446 | 322.343 | 0.30696 | 0.22332 | 0.20271 | 1.62175 | 1.95919 | 1.99915 | 2.498 | 3.47044 | 3.30975 | 22.73 | 79.7574 | 2.186E+10 | 251667 | 3.63649 | 0.54393 |
| *T. macrostachyum* | 215.473 | 0.09905 | 294.128 | 0.15734 | 0.20735 | 0.17962 | 1.19857 | 2.02082 | 1.16087 | 2.5672 | 1.27017 | 1.97007 | 7.43557 | 73.7942 | 9.584E+10 | 696912 | 0.25194 | 0.99903 |
| *T. microcarpum* | 329.016 | 0.11477 | 381.739 | 0.18297 | 0.26199 | 0.19902 | 1.14561 | 1.82966 | 2.31826 | 2.03773 | 2.50381 | 4.78405 | 18.1034 | 62.8291 | 4710.8274 | 2868.66 | 2.25331 | -0.0223 |
| *T. micromeria* | 280.284 | 0.04723 | 37.9302 | 0.25748 | 0.24974 | 0.10583 | 0.21458 | 1.46256 | 2.15514 | 2.1114 | 0.34693 | 1.47189 | 16.1621 | 91.6035 | 6.922E+09 | 139803 | -0.8126 | 1.72189 |
| *T. micropogon* | 262.369 | 0.09864 | 333.699 | 0.15827 | 0.22129 | 0.18351 | 0.94963 | 1.5966 | 2.76852 | 1.75661 | 3.81214 | 3.35151 | 19.146 | 74.4645 | 4.986E+10 | 545988 | 1.71956 | -0.7297 |
| *T. microcephalum* | 215.184 | 0.0968 | 269.181 | 0.19659 | 0.17414 | 0.13624 | 1.08233 | 1.8067 | 2.45343 | 1.84608 | 3.01489 | 3.77429 | 14.8424 | 73.8227 | 7.856E+10 | 734817 | 0.96892 | -0.5439 |

| | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *T. namaquense* | 254.591 | 0.11638 | 383.17 | 0.1873 | 0.12416 | 0.23797 | 1.22999 | 1.09915 | 2.47612 | 1.50375 | 3.28895 | 3.42093 | 13.9116 | 39.8592 | 6.869E+10 | 671154 | 0.69962 | -0.7942 |
| *T. nigromontanum* | 221.428 | 0.08861 | 434.968 | 0.19059 | 0.27659 | 0.20579 | 1.10898 | 1.59937 | 2.1128 | 2.08283 | 3.01217 | 4.55844 | 17.6727 | 90.49 | 1.78E+11 | 855797 | 2.17198 | -0.8664 |
| *T. nudicaule* | 270.028 | 0.13434 | 469.999 | 0.23385 | 0.24815 | 0.26326 | 1.39623 | 1.41684 | 3.40347 | 2.05775 | 3.29433 | 4.05147 | 16.7597 | 81.9082 | 3.971E+10 | 487752 | 3.34932 | -0.4601 |
| *T. occidentale* | 133.948 | 0.08265 | 425.22 | 0.15243 | 0.13105 | 0.16707 | 0.61354 | 0.85985 | 2.24153 | 1.64751 | 2.00161 | 4.71094 | 16.404 | 41.6685 | 3.362E+09 | 138840 | -0.8314 | -1.9406 |
| *T. paniculatum* | 201.818 | 0.11274 | 340.873 | 0.15471 | 0.23116 | 0.12872 | 0.46287 | 1.222 | 0.97135 | 1.82165 | 1.49622 | 1.59909 | 7.22257 | 43.5548 | 1.244E+10 | 439889 | -1.818 | 0.65268 |
| *T. paronychioides* | 206.571 | 0.06792 | 205.01 | 0.22122 | 0.3066 | 0.13673 | 1.07104 | 1.2496 | 2.27615 | 1.61699 | 0.8481 | 3.66911 | 3.51962 | 43.6058 | 8.218E+10 | 493669 | -1.1344 | 0.66371 |
| *T. patulum* | 340.282 | 0.11592 | 200.436 | 0.22874 | 0.22623 | 0.2695 | 0.91535 | 1.62289 | 1.98949 | 1.72717 | 1.16871 | 1.62518 | 17.2538 | 68.2381 | 3.142E+10 | 546798 | 1.14109 | 2.19376 |
| *T. penicillatum* | 192.23 | 0.12237 | 434.546 | 0.2145 | 0.20857 | 0.16933 | 0.736 | 1.33212 | 1.85526 | 2.29069 | 3.36811 | 4.10887 | 16.8089 | 89.1734 | 2.507E+10 | 542747 | 1.43311 | -1.1248 |
| *T. pinifolium* | 142.058 | 0.10983 | 398.745 | 0.15861 | 0.24806 | 0.14005 | 0.23776 | 1.23329 | 1.41661 | 1.84368 | 2.92753 | 2.90242 | 13.4655 | 79.9535 | 74510.827 | 2068.66 | -0.4216 | -0.7136 |
| *T. polycephalum* | 147.692 | 0.10632 | 201.148 | 0.70189 | 0.19022 | 0.32585 | 1.34459 | 1.1177 | 1.39115 | 0.90185 | 0.94266 | 0.37503 | 3.8375 | 56.2939 | 1.256E+09 | 120934 | 0.03986 | 3.31468 |
| *T. prostratum* | 160.122 | 0.02335 | 192.255 | 0.08552 | 0.16623 | 0.13466 | 0.53954 | 0.62905 | 1.07973 | 0.99096 | 0.91351 | 1.0538 | 4.11001 | 22.7222 | 6.794E+09 | 148250 | -4.382 | 0.03502 |
| *T. pseudovirgatum* | 204.834 | 0.12032 | 345.087 | 0.22568 | 0.20308 | 0.15539 | 0.83017 | 1.60005 | 0.85637 | 1.16981 | 1.66076 | 0.99212 | 6.45963 | 54.2057 | 7.562E+10 | 388325 | -1.209 | 1.44927 |
| *T. pubescens* | 309.84 | 0.12462 | 333.28 | 0.22369 | 0.26266 | 0.23121 | 0.96074 | 2.19912 | 2.03036 | 2.24353 | 1.35296 | 2.63901 | 10.8542 | 67.5234 | 2.602E+10 | 283896 | 1.6328 | 1.68276 |
| *T. pycnanthum* | 182.992 | 0.07991 | 635.173 | 0.22782 | 0.27548 | 0.18667 | 0.89751 | 1.15715 | 2.73301 | 3.44509 | 3.47798 | 3.41389 | 15.6806 | 96.3391 | 6.978E+09 | 265769 | 2.56182 | -2.0908 |
| *T. quartzicolum* | 149.644 | 0.0713 | 320.725 | 0.213 | 0.23866 | 0.18894 | 0.58794 | 0.28836 | 0.65965 | 1.194 | 1.98251 | 0.9957 | 5.29846 | 5.97752 | 1.003E+10 | 346885 | -3.3486 | 0.149 |
| *T. quinqueflorum* | 110.161 | 0.10511 | 274.159 | 0.19013 | 0.15296 | 0.13954 | 0.31647 | 0.89184 | 1.78215 | 1.1583 | 1.90335 | 2.00577 | 10.8868 | 62.8231 | 1.258E+10 | 169364 | -1.9887 | -0.1423 |
| *T. rariflorum* | 307.775 | 0.15621 | 180.06 | 0.27722 | 0.30941 | 0.26768 | 1.4912 | 2.23956 | 1.73833 | 2.63737 | 1.07844 | 1.88094 | 10.06 | 60.5542 | 789410463 | 48140.1 | 2.23527 | 3.04756 |
| *T. rhizomatum* | 45.6372 | 0.07002 | 60.2702 | 0.19727 | 0.3607 | 0.12055 | 0.497 | 0.80203 | 0.78586 | 0.66858 | 1.44834 | 0.84623 | 3.31621 | 7.62889 | 973410.83 | 3268.66 | -4.236 | 1.32641 |
| *T. rufescens* | 128.696 | 0.06736 | 87.2062 | 0.25548 | 0.29902 | 0.091 | 0.84523 | 0.88153 | 1.71593 | 1.19548 | 1.29465 | 1.15858 | 8.05264 | 19.2614 | 97410.827 | 268.656 | -2.7786 | 1.09996 |
| *T. nigroperianthum* | 183.588 | 0.00327 | 691.55 | 0.26197 | 0.1071 | 0.26832 | 1.47569 | 0.37123 | 1.65709 | 3.3234 | 3.21734 | 2.32167 | 14.2176 | 78.4889 | 9.398E+10 | 548112 | 1.16488 | -2.9533 |
| *T. scabrum* | 261.679 | 0.10528 | 380.74 | 0.20814 | 0.28492 | 0.17168 | 0.73737 | 1.56656 | 1.49834 | 1.78326 | 1.78425 | 2.14093 | 11.1247 | 79.5481 | 2.284E+10 | 454543 | 0.38117 | 1.0009 |
| *T. scandens* | 325.464 | 0.05467 | 314.059 | 0.13617 | 0.15308 | 0.21309 | 1.01867 | 1.30652 | 1.66465 | 0.92677 | 0.81296 | 2.92054 | 2.66858 | 28.2057 | 893204956 | 60117 | -1.8256 | 0.68472 |
| *T. schumannianum* | 267.965 | 0.07903 | 301.208 | 0.09947 | 0.23391 | 0.15619 | 0.85801 | 0.74339 | 0.37775 | 1.57661 | 1.09165 | 1.41401 | 4.59835 | 23.1784 | 7410.8274 | 4438.66 | -2.7977 | 0.79679 |
| *T. sedifolium* | 206.153 | 0.09101 | 318.884 | 0.11116 | 0.21151 | 0.1966 | 0.84828 | 1.32261 | 1.60959 | 1.74753 | 1.81132 | 1.37364 | 12.7115 | 63.9675 | 1.407E+10 | 423433 | -0.5065 | 0.43492 |
| *T. selagineum* | 77.9679 | 0.03209 | 591.867 | 0.31848 | 0.36611 | 0.22077 | 1.54876 | 0.81263 | 1.28073 | 3.2187 | 3.09257 | 2.83805 | 9.43825 | 27.8388 | 697410.83 | 2668.66 | 0.68589 | -1.7466 |
| *T. sertulariastrum* | 108.567 | 0.15022 | 197.498 | 0.18216 | 0.24638 | 0.23814 | 1.0922 | 2.16691 | 1.3554 | 2.85983 | 1.8785 | 4.31117 | 12.9791 | 45.2238 | 3.887E+10 | 373031 | 1.14848 | 0.47386 |
| *T. spicatum* | 190.506 | 0.11633 | 333.147 | 0.17713 | 0.21661 | 0.18706 | 0.9201 | 1.78701 | 1.42214 | 2.159 | 1.85678 | 2.29922 | 13.0166 | 73.1529 | 7.203E+10 | 457302 | 0.5094 | 0.58594 |
| *T. spinosum* | 317.049 | 0.20903 | 356.562 | 0.20543 | 0.33704 | 0.26585 | 1.2086 | 1.87413 | 3.7789 | 2.32184 | 2.18851 | 1.85698 | 13.6295 | 68.0816 | 6.814E+10 | 723807 | 3.47059 | 2.11785 |
| *T. spinulosum* | 181.976 | 0.11082 | 470.655 | 0.22256 | 0.22881 | 0.22886 | 0.86094 | 1.59321 | 1.83681 | 2.21202 | 2.52996 | 2.46567 | 10.2352 | 75.4416 | 8.326E+10 | 503053 | 1.02667 | -0.0571 |
| *T. squarrosum* | 174.24 | 0.08508 | 239.326 | 0.16646 | 0.1657 | 0.17766 | 1.06559 | 1.05242 | 2.17167 | 1.58935 | 1.35717 | 2.27888 | 7.46056 | 35.6491 | 1.198E+10 | 365525 | -1.4566 | 0.15089 |

| | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *T. stirtonii* | 275.508 | 0.04576 | 133.566 | 0.1744 | 0.19165 | 0.0841 | 1.22879 | 1.59145 | 1.14752 | 2.28189 | 0.5745 | 1.09884 | 9.77134 | 64.6398 | 2.199E+09 | 95861.4 | -1.2913 | 1.29041 |
| *T. strictum* | 198.967 | 0.11794 | 357.279 | 0.19059 | 0.22707 | 0.19926 | 0.98516 | 1.77132 | 2.3796 | 2.05779 | 3.23086 | 3.70384 | 19.0287 | 95.4656 | 2.95E+11 | 1115699 | 2.21577 | -0.4718 |
| *T. subnudum* | 204.449 | 0.11811 | 466.918 | 0.18614 | 0.20257 | 0.21424 | 0.96639 | 1.32354 | 2.42652 | 2.33427 | 3.49339 | 4.79028 | 18.6038 | 63.0931 | 1.05E+11 | 682793 | 1.90677 | -1.6181 |
| *T. susannae* | 96.8155 | 0.11266 | 225.271 | 0.07313 | 0.094 | 0.11509 | 0.3105 | 0.58307 | 0.99086 | 1.08122 | 1.62272 | 4.91692 | 2.51067 | 19.3169 | 1.084E+09 | 280087 | -4.0474 | -1.3343 |
| *T. translucens* | 179.533 | 0.10092 | 472.031 | 0.23559 | 0.21679 | 0.17774 | 0.78609 | 1.7642 | 1.70526 | 1.60098 | 2.388 | 1.40304 | 13.3455 | 85.0215 | 3.417E+10 | 354672 | 0.64402 | 0.36707 |
| *T. triflorum* | 288.536 | 0.0836 | 123.55 | 0.19238 | 0.07712 | 0.15763 | 1.12197 | 1.13616 | 1.55173 | 1.50902 | 2.44097 | 3.6798 | 2.61383 | 41.8499 | 6.597E+09 | 213294 | -1.6201 | -0.0745 |
| *T. umbelliferum* | 396.791 | 0.11469 | 508.119 | 0.19549 | 0.23342 | 0.21532 | 1.37498 | 1.66984 | 2.98151 | 1.80407 | 4.25871 | 5.27593 | 12.338 | 73.2493 | 4.954E+10 | 539570 | 3.09939 | -0.9875 |
| *T. urceolatum* | 182.892 | 0.17191 | 322.659 | 0.21813 | 0.20388 | 0.21877 | 1.1498 | 1.40034 | 3.57395 | 1.56376 | 1.67017 | 2.36658 | 11.3077 | 80.2174 | 5.104E+10 | 507347 | 1.44396 | 0.97268 |
| *T. virgatum* | 246.381 | 0.11771 | 391.46 | 0.20192 | 0.2519 | 0.20194 | 0.97884 | 1.66777 | 2.14195 | 1.94868 | 2.99262 | 3.54192 | 18.7502 | 84.5159 | 1.31E+11 | 680627 | 2.05012 | -0.1237 |
| *T. viridifolium* | 134.183 | 0.11925 | 136.557 | 0.09601 | 0.14853 | 0.14023 | 0.71538 | 0.53322 | 0.97149 | 0.50232 | 0.63259 | 0.60526 | 6.0676 | 12.5439 | 1.519E+09 | 88537.7 | -4.2421 | 1.24009 |
| *T. whitehillensis* | 371.101 | 0.1082 | 334.903 | 0.07675 | 0.19869 | 0.08855 | 0.75559 | 2.09177 | 2.21422 | 1.44845 | 3.42632 | 2.55445 | 6.71899 | 47.8048 | 5.141E+09 | 247627 | -0.1544 | 0.16849 |

**Appendix Table S5.3:** PCA loadings of the 14 environmental variables obtained from the ordination of *Thesium* species.

| Species | Soil depth | Soil EC | Elevation | Soil K | Soil N | Soil P | Soil pH | bio02 | bio03 | bio05 | bio08 | bio09 | bio15 | bio16 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *T. acuminatum* | -1.142 | -0.568 | -0.916 | -0.706 | -0.998 | -0.714 | -0.134 | -0.320 | -1.390 | -1.085 | -0.468 | -1.250 | -0.934 | -0.949 |
| *T. aggregatum* | 0.812 | 0.613 | 0.912 | 0.760 | 0.914 | 1.520 | 0.778 | 1.320 | 0.640 | 0.792 | -0.048 | 0.558 | 1.109 | 0.195 |
| *T. albomontanum* | -1.413 | -1.165 | 1.538 | 0.527 | 0.253 | 0.940 | 0.333 | -0.114 | 0.153 | 3.468 | 2.659 | 1.430 | -0.317 | -1.015 |
| *T. archeri* | -1.713 | -1.897 | -0.098 | 1.445 | 1.945 | -0.675 | 0.800 | -0.563 | -1.209 | -0.115 | 2.809 | 0.472 | 0.490 | 1.781 |
| *T. bathyschistum* | 0.222 | 0.059 | 0.134 | 0.986 | 0.008 | 0.543 | 0.874 | 0.165 | 0.296 | -0.168 | -0.379 | -0.402 | -0.022 | 0.595 |
| *T. brachygyne* | -0.285 | -0.235 | 0.810 | 1.026 | 1.359 | 0.836 | -0.876 | 0.641 | 0.250 | 0.126 | 0.106 | 0.412 | 0.319 | 0.932 |
| *T. capitatum* | -0.343 | 0.267 | 0.988 | 0.020 | 0.268 | 0.268 | -0.957 | 0.449 | 0.191 | 0.420 | 0.356 | 0.095 | 0.479 | 1.098 |
| *T. capitellatum* | -1.154 | 0.062 | 1.156 | 0.349 | -0.882 | -0.208 | 0.198 | 0.439 | -0.224 | 1.536 | -0.123 | -0.378 | -0.422 | 0.745 |
| *T. capituliflorum* | 0.730 | 0.022 | 0.845 | 0.755 | 0.356 | 0.468 | 0.199 | 0.743 | 0.618 | 0.167 | -0.317 | 0.200 | 0.279 | 0.967 |
| *T. carinatum* | -0.451 | -0.162 | 2.092 | 0.588 | -0.138 | 0.581 | -0.505 | 0.243 | 0.540 | 1.464 | 0.903 | 1.452 | 0.776 | 1.537 |
| *T. carinatumvar.pallidum* | -0.676 | 0.024 | 1.280 | 0.132 | 0.855 | 0.945 | -0.920 | -0.025 | -0.619 | 1.568 | 0.401 | 0.971 | 0.198 | 1.077 |
| *T. commutatum* | -0.184 | 0.424 | 0.002 | -1.259 | -0.269 | -0.054 | -0.381 | 0.433 | -0.459 | -0.568 | -0.097 | -0.558 | 0.195 | 0.083 |
| *T. densiflorum* | 0.176 | 0.403 | 0.625 | 0.013 | -0.100 | -0.124 | -0.695 | 0.602 | -0.376 | 0.619 | 0.108 | -0.128 | 0.281 | 0.654 |
| *T. disciflorum* | -1.784 | -1.709 | -0.388 | -0.794 | 0.952 | -1.189 | 0.060 | -0.116 | -1.051 | -0.126 | 2.252 | 1.394 | 1.031 | 0.675 |
| *T. dissitiflorum* | 0.879 | 0.075 | 0.679 | -0.847 | -0.555 | -1.087 | -0.499 | -1.498 | -0.212 | -0.116 | -0.501 | 1.065 | 0.614 | -0.359 |
| *T. diversifolium* | -1.986 | -1.184 | 0.170 | 1.712 | -0.252 | -2.686 | -0.102 | -1.367 | -1.612 | -1.182 | -0.488 | -1.337 | -0.976 | -0.546 |
| *T. dmmagiae* | -2.581 | -2.506 | -2.517 | -2.984 | -3.037 | -2.652 | -2.565 | -2.563 | -2.082 | -2.928 | -1.900 | -2.068 | -2.316 | -2.623 |
| *T. ecklonianum* | 2.398 | 0.150 | -0.893 | 2.042 | 2.056 | 0.540 | -0.282 | -1.174 | -0.061 | -1.540 | -0.798 | -1.287 | 0.380 | -0.287 |
| *T. elatius* | 0.652 | 3.352 | -1.003 | -0.318 | -0.068 | 1.100 | 0.798 | 1.100 | 2.853 | 0.254 | -1.050 | -1.047 | -0.472 | -0.468 |
| *T. ericaefolium* | -0.748 | 0.407 | 1.549 | -0.294 | -0.166 | 0.412 | 0.125 | 0.421 | 0.269 | 0.123 | 0.887 | 0.939 | 0.778 | 0.911 |
| *T. euphorbioides* | -0.314 | -0.637 | 0.561 | 0.257 | -0.357 | -0.117 | 0.043 | -0.083 | -0.033 | 0.331 | 0.335 | -0.623 | 0.404 | 1.007 |
| *T. euphrasioides* | 0.194 | -0.832 | -0.298 | 0.261 | 0.175 | -0.612 | -0.819 | -0.384 | -1.220 | -0.178 | -0.561 | -0.966 | -0.602 | 0.097 |
| *T. fallax* | 0.629 | -1.428 | -1.578 | -0.860 | -2.492 | -2.308 | -0.188 | 0.370 | 0.183 | -1.173 | -1.065 | -1.739 | 0.642 | 0.727 |
| *T. flexousum* | 0.649 | -0.369 | 0.624 | -0.228 | -0.309 | 0.966 | -0.050 | -0.523 | 0.541 | 0.146 | 0.114 | 1.497 | -0.139 | -1.105 |
| *T. foliosum* | -0.860 | 0.271 | -0.175 | -1.304 | -0.736 | 0.161 | -0.463 | -0.878 | 0.419 | -1.077 | -0.568 | -0.589 | -1.074 | -0.953 |
| *T. fragile* | 1.407 | 0.659 | -0.806 | 0.625 | -0.471 | 0.291 | 0.988 | 0.530 | 0.627 | -0.245 | -0.087 | 0.048 | 1.385 | 0.595 |
| *T. frisea* | 0.984 | 0.840 | -0.932 | 0.924 | 0.932 | 0.933 | -0.111 | 0.897 | 0.067 | 0.098 | -0.530 | -0.703 | 0.885 | 0.023 |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *T. friseavar.thunbergii* | 1.410 | 0.789 | -1.203 | -1.718 | 2.193 | 0.766 | -0.278 | 0.019 | -0.997 | -0.118 | -0.221 | -1.159 | 0.759 | -0.596 |
| *T. fructicosum* | -0.569 | -1.713 | -0.331 | -1.215 | -0.378 | -0.940 | 0.583 | -2.304 | 0.724 | -0.547 | -0.724 | -0.766 | -0.935 | -0.527 |
| *T. fruticulosum* | 1.224 | 0.391 | -0.434 | 0.139 | -0.704 | -0.468 | 0.600 | 1.211 | 0.279 | 0.576 | 0.078 | 0.121 | 1.064 | 0.855 |
| *T. funale* | 0.641 | 0.602 | -1.282 | 0.084 | 0.606 | -0.653 | -0.147 | 0.554 | -0.179 | -0.041 | -0.582 | -0.733 | 1.285 | 0.241 |
| *T. galioides* | -0.607 | -0.792 | -0.276 | -0.500 | -0.440 | -1.192 | 0.691 | -0.367 | -0.527 | -0.199 | 0.534 | 1.840 | -0.419 | -0.277 |
| *T. glomeruliflorum* | 0.418 | 1.423 | -0.217 | -0.467 | -0.923 | -0.301 | -0.259 | -0.426 | 0.524 | -1.115 | -0.455 | 1.279 | -0.390 | 0.252 |
| *T. gnidiaceum* | -0.578 | -0.655 | 0.124 | -0.477 | -0.239 | 0.758 | 0.489 | -0.659 | 0.571 | -0.479 | 1.435 | 0.101 | 0.341 | -0.955 |
| *T. hirtum* | -0.126 | 0.294 | 1.023 | 1.078 | -0.465 | 0.714 | 1.303 | 1.087 | 0.174 | 1.374 | -1.414 | 0.989 | 0.883 | 0.020 |
| *T. hispidulum* | -0.369 | -0.662 | 0.266 | 0.620 | 0.432 | -0.462 | -0.122 | -0.783 | -0.901 | 0.448 | -0.515 | -0.650 | -0.819 | -0.485 |
| *T. hispidulum.subglabrum* | -0.339 | -0.788 | -0.179 | 0.611 | 0.848 | -0.702 | -0.573 | -1.196 | -0.605 | 0.150 | -0.509 | -0.852 | -1.310 | -0.675 |
| *T. hollandii* | -0.432 | -1.147 | -0.359 | -0.782 | 1.290 | 0.901 | -0.050 | -0.534 | -1.771 | -1.539 | -0.896 | -0.651 | -2.224 | -1.269 |
| *T. imbricatum* | 1.461 | -0.638 | 2.077 | -0.116 | 0.957 | 0.853 | 1.775 | 1.978 | -0.286 | -0.371 | 1.814 | 0.336 | 1.226 | 0.557 |
| *T. junceum* | -0.013 | 0.322 | -0.452 | -0.470 | -0.026 | -0.856 | 0.290 | 0.253 | 1.184 | -0.301 | -0.265 | 0.755 | 0.230 | -0.432 |
| *T. juncifolium* | 0.458 | -0.729 | 0.595 | 0.668 | -0.461 | -0.174 | -0.046 | -0.510 | -0.431 | 0.427 | -0.252 | 0.085 | 0.773 | 0.585 |
| *T. karooicum* | -0.897 | -1.271 | 0.671 | 0.666 | -0.149 | -0.262 | 1.057 | -1.893 | 0.836 | 0.337 | 2.472 | 1.055 | -0.433 | -1.427 |
| *T. leptocaule* | 0.659 | -0.221 | 0.002 | -0.466 | 0.821 | -0.284 | 0.474 | 0.294 | 0.241 | -0.817 | -0.073 | 0.964 | 0.435 | -0.714 |
| *T. litoreum* | 1.930 | 2.288 | -0.129 | 0.551 | -0.733 | 2.297 | 1.919 | 1.208 | -0.778 | 0.994 | -0.777 | -0.758 | -1.335 | 0.010 |
| *T. longicaule* | 1.593 | 0.702 | -0.083 | 2.488 | 0.024 | 0.481 | 2.493 | 1.248 | 0.276 | 1.159 | 1.228 | 0.456 | 2.207 | 0.877 |
| *T. macrostachyum* | -0.113 | 0.007 | -0.321 | -0.615 | -0.246 | 0.009 | 0.967 | 1.382 | -0.927 | 1.275 | -0.852 | -0.597 | -0.885 | 0.611 |
| *T. microcarpum* | 1.257 | 0.437 | 0.419 | -0.084 | 0.677 | 0.405 | 0.775 | 0.967 | 0.734 | 0.383 | 0.314 | 1.614 | 1.272 | 0.121 |
| *T. micromeria* | 0.669 | -1.412 | -2.486 | 1.462 | 0.470 | -1.497 | -2.583 | 0.170 | 0.500 | 0.507 | -1.725 | -0.988 | 0.879 | 1.406 |
| *T. micropogon* | 0.453 | -0.005 | 0.013 | -0.596 | -0.010 | 0.089 | 0.068 | 0.461 | 1.381 | -0.091 | 1.551 | 0.488 | 1.482 | 0.641 |
| *T. minus* | -0.116 | -0.055 | -0.532 | 0.199 | -0.807 | -0.876 | 0.547 | 0.917 | 0.929 | 0.060 | 0.797 | 0.820 | 0.612 | 0.612 |
| *T. namaquense* | 0.359 | 0.481 | 0.431 | 0.006 | -1.650 | 1.201 | 1.080 | -0.620 | 0.961 | -0.518 | 1.056 | 0.543 | 0.424 | -0.905 |
| *T. nigromantanum* | -0.041 | -0.279 | 0.868 | 0.074 | 0.923 | 0.544 | 0.643 | 0.467 | 0.439 | 0.459 | 0.795 | 1.437 | 1.185 | 1.357 |
| *T. nudicaule* | 0.545 | 0.973 | 1.164 | 0.972 | 0.443 | 1.717 | 1.680 | 0.070 | 2.293 | 0.416 | 1.062 | 1.038 | 1.000 | 0.973 |
| *T. occidentale* | -1.096 | -0.442 | 0.786 | -0.717 | -1.534 | -0.247 | -1.144 | -1.139 | 0.624 | -0.275 | -0.161 | 1.556 | 0.928 | -0.824 |
| *T. paniculatum* | -0.277 | 0.381 | 0.073 | -0.670 | 0.156 | -1.030 | -1.688 | -0.353 | -1.199 | 0.018 | -0.639 | -0.888 | -0.928 | -0.740 |
| *T. paronychioides* | -0.220 | -0.846 | -1.074 | 0.710 | 1.430 | -0.866 | 0.506 | -0.293 | 0.674 | -0.327 | -1.251 | 0.738 | -1.677 | -0.738 |
| *T. patulum* | 1.393 | 0.469 | -1.113 | 0.866 | 0.073 | 1.844 | -0.055 | 0.518 | 0.262 | -0.141 | -0.948 | -0.868 | 1.100 | 0.363 |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *T. penicillatum* | -0.393 | 0.645 | 0.865 | 0.570 | -0.225 | -0.201 | -0.702 | -0.114 | 0.070 | 0.809 | 1.131 | 1.083 | 1.010 | 1.298 |
| *T. pinifolium* | -0.998 | 0.302 | 0.562 | -0.589 | 0.442 | -0.799 | -2.500 | -0.328 | -0.560 | 0.055 | 0.715 | 0.135 | 0.334 | 0.886 |
| *T. prostratum* | -0.780 | -2.066 | -1.182 | -2.104 | -0.940 | -0.908 | -1.411 | -1.640 | -1.044 | -1.382 | -1.190 | -1.317 | -1.557 | -1.670 |
| *T. pseudovirgatum* | -0.241 | 0.589 | 0.109 | 0.802 | -0.318 | -0.485 | -0.362 | 0.468 | -1.364 | -1.081 | -0.483 | -1.365 | -1.082 | -0.264 |
| *T. pubescens* | 1.026 | 0.707 | 0.009 | 0.761 | 0.688 | 1.063 | 0.109 | 1.769 | 0.321 | 0.730 | -0.774 | -0.071 | -0.194 | 0.331 |
| *T. pycnanthum* | -0.505 | -0.518 | 2.559 | 0.846 | 0.905 | 0.153 | -0.120 | -0.494 | 1.330 | 2.756 | 1.235 | 0.537 | 0.782 | 1.618 |
| *T. quartzicolum* | -0.907 | -0.753 | -0.097 | 0.539 | 0.283 | 0.200 | -1.236 | -2.380 | -1.647 | -1.040 | -0.179 | -1.363 | -1.317 | -2.418 |
| *T. quinqueflorum* | -1.383 | 0.173 | -0.490 | 0.065 | -1.164 | -0.809 | -2.216 | -1.070 | -0.035 | -1.100 | -0.254 | -0.569 | -0.187 | 0.121 |
| *T. rariflorum* | 1.001 | 1.572 | -1.285 | 1.871 | 1.477 | 1.807 | 2.022 | 1.857 | -0.098 | 1.394 | -1.034 | -0.667 | -0.355 | 0.019 |
| *T. rhizomatum* | -2.162 | -0.788 | -2.297 | 0.213 | 2.343 | -1.197 | -1.564 | -1.265 | -1.466 | -1.926 | -0.684 | -1.480 | -1.718 | -2.345 |
| *T. scabrum* | 0.445 | 0.177 | 0.410 | 0.438 | 1.064 | -0.153 | -0.697 | 0.395 | -0.443 | -0.046 | -0.366 | -0.463 | -0.139 | 0.868 |
| *T. scandens* | 1.214 | -1.209 | -0.153 | -1.054 | -1.162 | 0.693 | 0.318 | -0.169 | -0.204 | -1.491 | -1.285 | 0.150 | -1.849 | -1.426 |
| *T. schumannianum* | 0.521 | -0.542 | -0.262 | -1.815 | 0.203 | -0.469 | -0.262 | -1.392 | -2.052 | -0.395 | -1.021 | -1.034 | -1.459 | -1.650 |
| *T. sedifolium* | -0.225 | -0.214 | -0.112 | -1.573 | -0.175 | 0.356 | -0.297 | -0.134 | -0.283 | -0.107 | -0.341 | -1.066 | 0.182 | 0.172 |
| *T. sertulariastrum* | -1.402 | 1.408 | -1.138 | -0.100 | 0.413 | 1.204 | 0.583 | 1.699 | -0.648 | 1.769 | -0.277 | 1.242 | 0.236 | -0.665 |
| *T. spicatum* | -0.414 | 0.480 | 0.008 | -0.205 | -0.089 | 0.161 | -0.038 | 0.874 | -0.552 | 0.587 | -0.298 | -0.338 | 0.243 | 0.582 |
| *T. spinosum* | 1.113 | 3.018 | 0.206 | 0.382 | 1.944 | 1.770 | 1.003 | 1.063 | 2.832 | 0.862 | 0.016 | -0.686 | 0.367 | 0.356 |
| *T. spinulosum* | -0.517 | 0.329 | 1.170 | 0.738 | 0.117 | 1.015 | -0.251 | 0.453 | 0.043 | 0.677 | 0.339 | -0.208 | -0.319 | 0.684 |
| *T. squarrosum* | -0.610 | -0.376 | -0.784 | -0.426 | -0.949 | -0.031 | 0.487 | -0.721 | 0.524 | -0.373 | -0.770 | -0.354 | -0.880 | -1.093 |
| *T. stirtonii* | 0.612 | -1.453 | -1.678 | -0.261 | -0.511 | -1.941 | 1.076 | 0.450 | -0.946 | 0.794 | -1.510 | -1.281 | -0.413 | 0.202 |
| *T. strictum* | -0.312 | 0.524 | 0.212 | 0.074 | 0.087 | 0.410 | 0.197 | 0.840 | 0.823 | 0.417 | 1.002 | 0.765 | 1.459 | 1.579 |
| *T. subnudum* | -0.246 | 0.529 | 1.138 | -0.018 | -0.326 | 0.716 | 0.129 | -0.132 | 0.890 | 0.883 | 1.250 | 1.619 | 1.373 | 0.133 |
| *T. susannae* | -1.544 | 0.379 | -0.903 | -2.362 | -2.160 | -1.308 | -2.237 | -1.740 | -1.171 | -1.230 | -0.519 | 1.718 | -1.881 | -1.823 |
| *T. translucens* | -0.546 | 0.058 | 1.181 | 1.008 | -0.086 | -0.029 | -0.522 | 0.825 | -0.146 | -0.354 | 0.205 | -1.043 | 0.310 | 1.112 |
| *T. triflorum* | 0.769 | -0.416 | -1.762 | 0.111 | -2.445 | -0.440 | 0.690 | -0.539 | -0.366 | -0.509 | 0.255 | 0.746 | -1.860 | -0.816 |
| *T. umbelliferum* | 2.075 | 0.435 | 1.486 | 0.176 | 0.194 | 0.738 | 1.603 | 0.620 | 1.687 | -0.011 | 1.973 | 2.000 | 0.106 | 0.587 |
| *T. urceolatum* | -0.506 | 2.002 | -0.080 | 0.646 | -0.304 | 0.809 | 0.791 | 0.034 | 2.537 | -0.417 | -0.474 | -0.285 | -0.102 | 0.898 |
| *T. virgatum* | 0.260 | 0.518 | 0.501 | 0.309 | 0.506 | 0.465 | 0.174 | 0.615 | 0.481 | 0.233 | 0.776 | 0.638 | 1.402 | 1.090 |
| *T. viridifolium* | -1.093 | 0.560 | -1.653 | -1.887 | -1.239 | -0.795 | -0.777 | -1.849 | -1.199 | -2.206 | -1.455 | -1.669 | -1.162 | -2.125 |
| *T. whitehillensis* | 1.765 | 0.257 | 0.023 | -2.286 | -0.392 | -1.850 | -0.632 | 1.536 | 0.585 | -0.611 | 1.186 | -0.138 | -1.030 | -0.550 |

**Appendix Table S5.4:** The eigen values of the environmental variables obtained from the PCA.

| | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 | PC7 | PC8 | PC9 | PC10 | PC11 | PC12 | PC13 | PC14 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| soil_depth | -0.206 | 0.420 | -0.126 | 0.134 | -0.369 | 0.140 | -0.316 | 0.420 | -0.401 | 0.009 | 0.108 | 0.347 | -0.110 | -0.101 |
| soil_EC | -0.228 | 0.375 | -0.250 | -0.040 | 0.512 | 0.086 | 0.045 | -0.142 | 0.273 | -0.251 | 0.260 | 0.351 | 0.312 | -0.161 |
| elev | -0.257 | -0.368 | -0.065 | -0.191 | 0.233 | -0.116 | -0.107 | 0.657 | 0.041 | 0.163 | 0.191 | -0.092 | 0.319 | 0.269 |
| K | -0.256 | 0.056 | 0.457 | -0.112 | -0.172 | -0.031 | 0.624 | 0.119 | -0.057 | -0.360 | 0.261 | 0.123 | -0.137 | 0.205 |
| N | -0.178 | 0.073 | 0.547 | -0.368 | 0.023 | 0.481 | -0.297 | -0.248 | -0.092 | 0.266 | 0.120 | -0.090 | 0.210 | -0.036 |
| P | -0.298 | 0.203 | -0.115 | -0.467 | 0.222 | 0.033 | -0.037 | 0.173 | 0.000 | -0.230 | -0.437 | -0.337 | -0.421 | -0.149 |
| pH | -0.269 | 0.160 | -0.184 | -0.252 | -0.606 | -0.271 | 0.103 | -0.105 | 0.318 | 0.108 | -0.073 | -0.167 | 0.411 | -0.163 |
| bio02 | -0.316 | 0.246 | 0.055 | 0.224 | 0.031 | -0.326 | -0.359 | -0.243 | 0.183 | 0.046 | 0.245 | -0.226 | -0.280 | 0.515 |
| bio03 | -0.280 | 0.057 | -0.368 | 0.140 | 0.052 | 0.391 | 0.472 | -0.092 | -0.080 | 0.559 | -0.005 | -0.084 | -0.144 | 0.174 |
| bio05 | -0.315 | -0.127 | 0.139 | -0.083 | 0.191 | -0.515 | 0.039 | -0.238 | -0.380 | 0.275 | -0.308 | 0.421 | 0.033 | -0.075 |
| bio08 | -0.227 | -0.471 | -0.076 | -0.110 | -0.202 | 0.203 | -0.180 | -0.068 | 0.466 | -0.017 | 0.009 | 0.470 | -0.386 | -0.049 |
| bio09 | -0.228 | -0.386 | -0.349 | -0.074 | -0.083 | 0.048 | -0.082 | -0.326 | -0.480 | -0.354 | 0.356 | -0.231 | 0.035 | -0.110 |
| bio15 | -0.320 | -0.111 | 0.077 | 0.432 | -0.047 | 0.280 | -0.067 | -0.028 | 0.002 | -0.344 | -0.551 | -0.016 | 0.346 | 0.256 |
| bio16 | -0.313 | -0.102 | 0.267 | 0.484 | 0.100 | -0.076 | 0.028 | 0.140 | 0.135 | 0.107 | 0.143 | -0.270 | -0.096 | -0.647 |

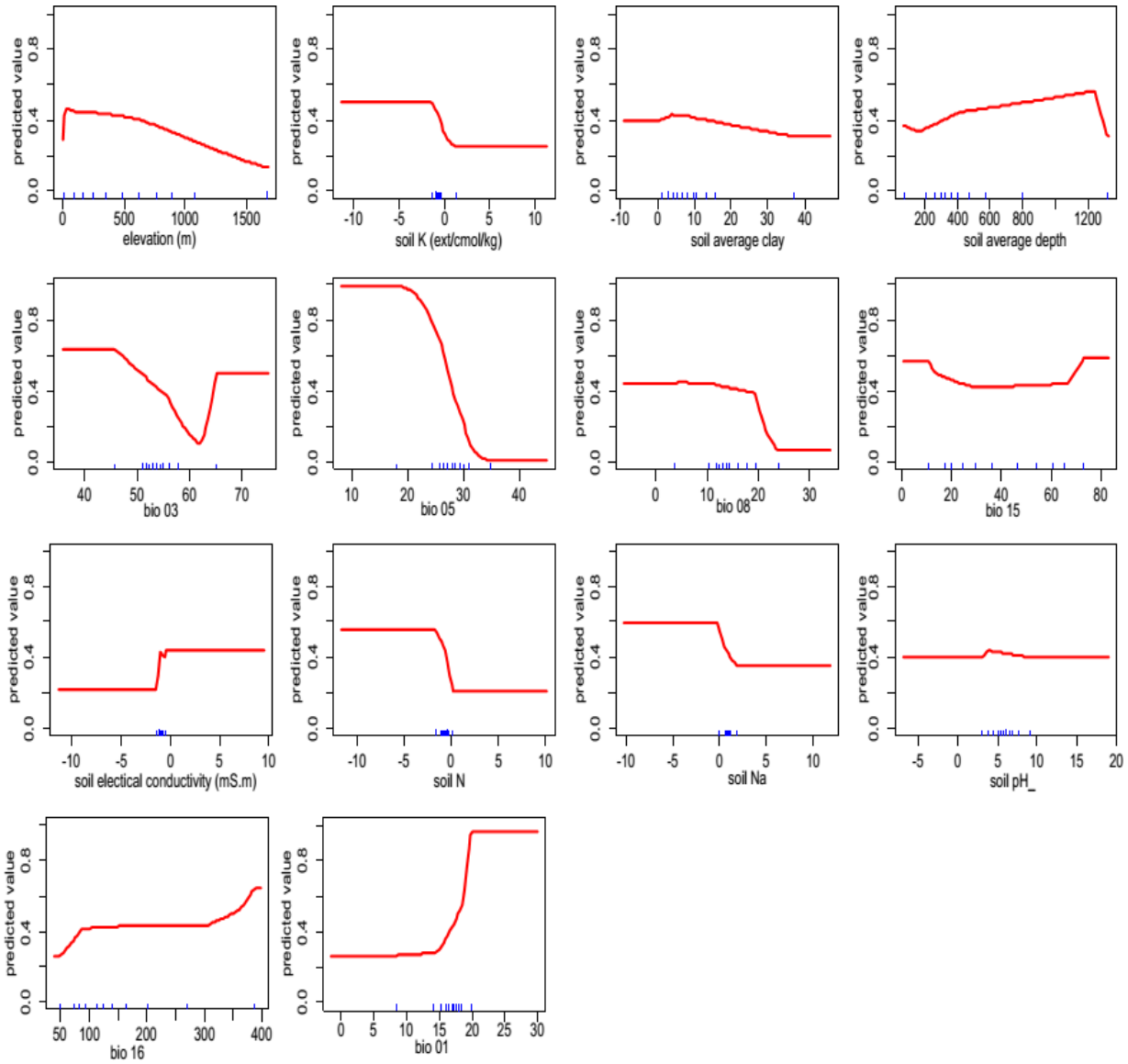
**Appendix Table S5.5:** The AUC values retained from the Maxent outputs and the percentage contribution of the environmental variables in the final model. The two most important variables for each species distribution are indicated in bold.

| Species | AUC value | soil clay | soil depth | soil EC | elev-ation | soil K | soil N | soil P | soil pH | bio 02 | bio 03 | bio 05 | bio 08 | bio 09 | bio 15 | bio 16 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *T. acuminatum* | 0.996 | 0 | 1.4 | 2 | 0.3 | 0.1 | 7.8 | 1.1 | 0.8 | **52.3** | 0.8 | 2.2 | 0.1 | 0 | 8.5 | **22.6** |
| *T. aggregatum* | 0.938 | 0.2 | 1.1 | 2.6 | 1.5 | 0.2 | 1 | 0.5 | 3.3 | **53.7** | 1.4 | 0 | 2.2 | 0.9 | 8 | **23.2** |
| *T. albomontanum* | 0.985 | 4 | 0.2 | 0 | **14** | 0 | 0.2 | 1.2 | 0 | 6.7 | 6.3 | 0 | **52.5** | 6 | 9 | 0 |
| *T. annulatum* | 0.901 | 9.6 | 0 | 0 | 0 | 2.6 | 0 | 0 | **38.2** | 0 | 0.9 | 0 | **44.1** | 0 | 0 | 4.6 |
| *T. archeri* | 0.907 | **5.8** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | **94.2** | 0 | 0 | 0 | 0 | 0 |
| *T. bathyschistum* | 0.959 | 3.3 | 2.8 | 0 | 0.3 | 0.6 | 9.1 | 0 | 0 | **58.1** | 0 | 0.2 | 0.1 | 0 | 8.5 | **17** |
| *T. brachygyne* | 0.948 | 0 | 4 | 0 | 0.6 | 0.1 | 8.7 | 0.2 | **44.8** | 8.2 | 0.2 | 2.2 | 3.3 | 1 | 7.7 | **19** |
| *T. capitatum* | 0.952 | 0.6 | 1.7 | 0.8 | 0.6 | 0.1 | 0.2 | 0.3 | **35.8** | 13.8 | 6.3 | 12.5 | 2.7 | 1.5 | 2.3 | **20.8** |
| *T. capitellatum* | 0.928 | 0.6 | 1.5 | 0.1 | 0 | 0 | 1.6 | 1 | 14.1 | 3.3 | 0.2 | **14.2** | 13.7 | 0 | 0 | **49.4** |
| *T. capituliflorum* | 0.941 | 4.2 | 0.1 | 0.9 | 0.9 | 0.2 | 3.5 | 0.1 | 13.1 | **15.9** | 2.9 | 4.5 | 3.2 | 1.8 | 5 | **43.8** |
| *T. carinatum* | 0.928 | 1.4 | 2.1 | 2.5 | 1.4 | 0.5 | 3.4 | 0.4 | **47.7** | 8.2 | 0.1 | **13.6** | 4.1 | 2.4 | 0 | 12.1 |
| *T. commutatum* | 0.967 | 0.7 | 0.3 | 0.9 | 0.4 | 1.7 | 1.9 | 0.2 | 2.3 | **48.8** | 1.2 | 6.6 | 0.6 | 2.5 | 2.5 | **29.6** |
| *T. densiflorum* | 0.958 | 0.4 | 0.2 | 0 | 0 | 0.1 | 3.6 | 0.1 | 14.9 | **24.2** | 1.3 | 1.7 | 0.2 | 0.1 | 0.7 | **52.4** |
| *T. disciflorum* | 0.901 | 0 | 20 | 0 | 0 | 0 | 0 | 0 | **46.9** | 0 | **33.2** | 0 | 0 | 0 | 0 | 0 |
| *T. dissitiflorum* | 0.909 | 1.6 | 0 | 0 | 0 | 0.3 | 0 | 0.9 | 0 | 3.3 | **21.3** | 0 | **72.5** | 0 | 0 | 0 |
| *T. diversifolium* | 0.937 | 0 | 1.3 | 0.2 | 0 | 0 | **43.7** | 5.3 | 15.4 | 0 | 18.8 | 0.5 | 0 | 0.1 | **14.7** | 0 |
| *T. dmmagiae* | 0.994 | **21.8** | 9.5 | **18.3** | 6.4 | 0 | 0 | 1.7 | 0 | 12.3 | 5.2 | 0 | 9.3 | 4.1 | 3.3 | 8.3 |
| *T. ecklonianum* | 0.943 | 0 | 0 | 0.2 | 4 | 0 | 21.9 | 0 | 0.3 | **32.7** | 0 | 0 | 0 | 0.4 | 8.2 | **32.3** |
| *T. elatius* | 0.933 | 7.7 | 4 | 0.6 | **40.7** | 0.3 | 0.7 | 0.2 | 0.3 | 0 | 12.8 | 0 | 1.5 | 0 | **29.6** | 1.4 |
| *T. ericaefolium* | 0.94 | 1.1 | 2.6 | 4.1 | 3.6 | 0 | 0.1 | 0.7 | 19 | **52.5** | 3.2 | 3.5 | 1.6 | 2 | 4 | 2.3 |
| *T. euphorbioides* | 0.957 | 2.1 | 0.3 | 2 | 0.5 | 0.2 | 0 | 1.3 | 11.5 | **27.9** | 2.4 | 7.7 | 0 | 5.6 | 3.7 | **34.7** |
| *T. euphrasioides* | 0.972 | 0 | 0.6 | 2.6 | 1.4 | 0 | 0.2 | 0 | **8.6** | 3.1 | 0.2 | 3.4 | 0 | 0.3 | 0.7 | **78.8** |
| *T. fallax* | 0.917 | **12.2** | 0.6 | 4.5 | 11.1 | 0 | 0.9 | 1.5 | 0.6 | **47.3** | 0 | 15.1 | 2.6 | 0 | 0 | 3.5 |
| *T. flexuosum* | 0.904 | 2 | 1.2 | 0.7 | 9.6 | 0.5 | 0 | 0.5 | 2.2 | 11.6 | 0.8 | 0 | 0.4 | 0.9 | **52.5** | **16.9** |
| *T. foliosum* | 0.964 | 0.8 | 0.5 | 0.1 | 0.1 | 0.5 | 2.3 | 0.1 | 3.4 | 17.8 | 0.1 | 0 | 0.8 | **34.9** | 5.2 | **33.3** |

| | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *T. fragile* | 0.937 | 1 | 1.2 | 1.3 | 10 | 0.3 | **4.3** | 0.6 | 0.7 | **66** | 1.4 | 2.3 | 0.9 | 3.9 | 2.5 | 3.9 |
| *T. frisea* | 0.936 | 0.3 | 1.2 | 1.2 | 13.2 | 0.1 | 0.2 | 0 | 3.2 | **30.7** | 0.7 | 0.3 | 0 | 7.7 | 4 | **36.9** |
| *T. fructicosum* | 0.912 | 0.5 | 0 | 0.3 | 1.3 | 0 | 0 | 0 | 0 | 5.1 | **26.6** | 0 | 0.8 | **47.1** | **13.2** | 1.9 |
| *T. fruticulosum* | 0.932 | 0.6 | 1.8 | 1.3 | 2.4 | 1 | 1 | 4.3 | 2.2 | **49.8** | 8.2 | 2.2 | 0.2 | 0.8 | 0.2 | 18.2 |
| *T. funale* | 0.958 | 1.9 | 2 | 0.1 | 1.6 | 0 | 1.3 | 1.5 | 3.1 | **63.2** | 2 | 2.9 | 0.4 | 3.7 | 0.2 | **23.9** |
| *T. galioides* | 0.904 | 2.3 | 1.5 | 7.5 | 4.8 | 0.7 | 4.4 | 4.1 | 0.9 | 8.6 | **10.1** | 1.7 | 4.7 | 0.8 | 5.3 | **10.9** |
| *T. glomeratum* | 0.923 | 0 | 0 | 0 | **46.8** | 0 | **51.4** | 1.8 | 0 | 0 | 0 | 0 | 0 | 0 | **38.2** | 9.7 |
| *T. glomeruliflorum* | 0.955 | 0 | 0.2 | 14.1 | 0.1 | 0.3 | 0.2 | 1.4 | **29.1** | 8.3 | 0 | 3.4 | 1.4 | 4.2 | 0 | 0 |
| *T. gnidiaceum* | 0.966 | 0 | 9.7 | 1.4 | 0 | 0 | 16.2 | 5.3 | **20.1** | 0.8 | 0 | 0 | 0 | 0 | **34.5** | 3 |
| *T. hillianum* | 0.938 | 0 | **51.5** | 0.4 | 0 | 48 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 46.6 | 0 |
| *T. hirtum* | 0.946 | 2.5 | 0.2 | 1.6 | 3.8 | 0.1 | 0.3 | 0.1 | 2.2 | **64.9** | 0 | 6.9 | 3.7 | 3.5 | 0 | 0 |
| *T. hispidulum* | 0.953 | 1.3 | 0.5 | 0.5 | 6.1 | 11.6 | 0.9 | 0.4 | 2.3 | 0 | 3 | 0.3 | 2.2 | 0.5 | 2.9 | **7.4** |
| *T. hollandii* | 0.985 | 0 | 0 | 0 | 0.6 | 0 | 0.7 | 0 | 0 | **9** | 3.2 | 0 | 0.4 | 2.5 | **37.4** | **33** |
| *T. imbricatum* | 0.980 | 0 | 0 | 0 | 0 | 0.5 | 26 | 0 | 0 | 0 | **26.2** | **47.3** | 0 | 0 | **43.5** | **36.2** |
| *T. impeditum* | 0.927 | 0.5 | 0 | **40.1** | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | 4.7 | 0 | 18.7 | **80.2** | 3.3 |
| *T. junceum* | 0.908 | 0.7 | 0.6 | 0.4 | 1.6 | 0.6 | 3 | 2.6 | 1 | **21.7** | 0.3 | 0 | 7.8 | 12.4 | 0 | 0 |
| *T. juncifolium* | 0.958 | 0.4 | 6 | 0.2 | 0 | 7.2 | 3.6 | 0.2 | 10.6 | 10.7 | **20.1** | 0 | 8.7 | 4.2 | 0 | **36** |
| *T. karooicum* | 0.831 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0.7 | **44.8** | 0 | 0 | 0 | 11 | **36.3** |
| *T. leptocaule* | 0.908 | 2.9 | 0 | 4.7 | 6.2 | 2.1 | 4.7 | 3.4 | 0 | **33.2** | 0.1 | 0.9 | 0.1 | 2.1 | 7.1 | **21** |
| *T. leptostachyum* | 0.801 | 0 | **19.2** | 0 | 0 | 0 | 0 | 8.7 | 0 | 0 | 4.9 | 0 | 0 | 0 | **52.8** | 1.6 |
| *T. lisae-mariae* | 0.836 | 0.3 | **16** | 0 | 0 | 0 | 10.1 | 0 | 0 | 0 | **50.2** | 9.9 | 0 | 5.6 | **32** | 7.6 |
| *T. litoreum* | 0.924 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | 0 | **33.9** | 2.5 | 0 | 0 | 0 | 0.1 | **67.1** |
| *T. longicaule* | 0.886 | 0 | 0 | 0 | 0 | 0 | 0.7 | 0 | 0 | **69.1** | 0 | 0 | 0 | 0 | 6.5 | 1.4 |
| *T. macrostachyum* | 0.935 | 0.7 | 12.8 | 0 | 0.5 | 0.1 | 0 | 1.3 | 8.4 | 0.7 | 6.7 | 0 | 0.4 | 1.3 | **33.3** | 30.2 |
| *T. microcarpum* | 0.853 | 6.2 | 2.9 | 0.8 | 1.4 | 0.6 | 0.1 | 1.6 | 0.4 | **47.1** | 1.1 | 3.2 | 2.7 | 2.9 | 0 | **30.2** |
| *T. microcephalum* | 0.960 | 0 | 0 | 0 | 88.9 | 0 | 0 | 0 | 0 | 0 | 0 | 11.1 | 0 | 0 | **37.3** | **29.8** |
| *T. micromeria* | 0.948 | 0 | 0 | 0 | **51.3** | 0.2 | 0 | 0 | 8.9 | 0 | 0.1 | 0 | 10.7 | 0 | **27** | 2.1 |
| *T. micropogon* | 0.911 | 0 | 0 | 0 | 0 | 8.1 | **59.2** | 0 | 0 | 5.3 | 0 | 0.1 | 0 | 0 | 0 | 0 |
| *T. minus* | 0.913 | **6.8** | 0.3 | 0 | 1.5 | 4.6 | 0 | 0 | 0.2 | 5.9 | 0.7 | 1.6 | 0 | 0 | 0 | **28.8** |
| *T. namaquense* | 0.924 | 12.7 | 0.7 | 0 | 14.9 | 0 | 0 | 0.8 | 0 | 4.6 | 6.2 | 0 | **19.3** | 3 | 0 | **27.3** |

| | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *T. nigromantanum* | 0.928 | 0.5 | 1.4 | 2.1 | 0.8 | 6.8 | **7.6** | 1.2 | 8.9 | **58.2** | 1.8 | 0.6 | 0.3 | 0.4 | 3.9 | **69.8** |
| *T. nigroperianthum* | 0.993 | **24.3** | 0 | 8.6 | 0 | 0 | **60.1** | 0 | 0 | 6.2 | 0 | 0 | 0 | 0 | 7.8 | **30** |
| *T. nudicaule* | 0.9 | 8 | 7.9 | 0.2 | 0.5 | 5.2 | 2.5 | 1.4 | 3.7 | **27.5** | 0.7 | 0 | **22.3** | 0.6 | 3.2 | 6.1 |
| *T. occidentale* | 0.915 | 0 | 0 | 1.8 | 0 | 1.8 | 0 | 0 | **62.7** | 1.6 | 0 | 0 | **32.1** | 0 | 0 | 0 |
| *T. paniculatum* | 0.995 | 0.6 | 0 | 1.1 | 0 | 0.1 | 0.2 | 3.2 | 10.5 | **20** | 0.7 | 3 | 0.4 | 0 | 2.8 | 16.6 |
| *T. paronychioides* | 0.95 | 0.3 | 0 | 0 | 7.8 | 0 | **29.4** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *T. patulum* | 0.957 | 0 | 0.5 | 1.1 | **39.1** | 0.5 | 1.4 | 1 | 1.3 | 2.9 | 6.6 | 0 | 3.2 | 6.7 | 0.8 | **59.3** |
| *T. penicillatum* | 0.958 | 0.6 | 0.1 | 5.8 | 0.3 | 0.2 | 0 | 1.8 | **31** | **37.6** | 0 | 4.7 | 0 | 0.4 | **54.1** | 0.6 |
| *T. pinifolium* | 0.989 | 0.7 | 0.5 | 0 | 0.1 | 0 | 0 | 14.8 | **61.6** | 2.5 | 0.1 | 0.9 | 0 | 0.8 | 4.2 | **31.5** |
| *T. polycephalum* | 0.901 | 0.1 | 2.8 | **13** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.3 | 0 | 6.6 | 3.4 | 14.3 |
| *T. prostratum* | 0.99 | 0 | 0 | 5.2 | 0 | 19.7 | 14.8 | 0 | **23.1** | 0 | 1.2 | 0 | **30.7** | 0 | 0 | **18.1** |
| *T. pseudovirgatum* | 0.993 | 0.9 | 1 | 0 | 0.8 | 0.4 | 3.6 | 0.5 | 3.3 | **35** | 1.2 | 1.5 | 0.1 | 2.8 | **77.2** | 0 |
| *T. pubescens* | 0.956 | 4.6 | 5.1 | 0.3 | 3.9 | 0.1 | 11.7 | 0 | 1.3 | 10.5 | 2.2 | 0.5 | 0.2 | 0.3 | 5.1 | 0.4 |
| *T. pycnanthum* | 0.955 | 4.7 | 0.5 | 0 | 8.1 | 0.9 | 1.5 | 0 | 0.6 | 4.4 | 0.8 | 7.3 | **12.9** | 0.4 | 11.8 | **37.1** |
| *T. quartzicolum* | 0.973 | 1.4 | 0 | 11.6 | 0 | 0 | 0 | 0 | 0 | **45.4** | 9.4 | 0 | 1.7 | **13** | **37.3** | **21.9** |
| *T. quinqueflorum* | 0.992 | 2.1 | 0.6 | 0 | 0.7 | 1.3 | 0 | 0 | 22.7 | **23.7** | 1.6 | 6.7 | 1.1 | 0 | 0 | **57.8** |
| *T. rariflorum* | 0.961 | 0 | 0 | 0 | 6.1 | 0 | **15.4** | 1.5 | 0 | 1.6 | 0 | 0 | 0.5 | 0 | 6.6 | 10.9 |
| *T. rhizomatum* | 0.981 | 0 | 11.5 | 13.3 | **29.1** | 0 | 0 | 0.7 | 0 | 0 | 8.5 | 6.9 | 0 | **14.9** | 0 | **39.5** |
| *T. rufescens* | 0.988 | 4.1 | 11.4 | 0 | **50.2** | 0 | 0 | 0 | 0 | **23.4** | 0.2 | 0 | 0 | 3.1 | 3.2 | **71.6** |
| *T. sawae* | 0.943 | 0.1 | 0.6 | 0.1 | 0.4 | **19.3** | 1.6 | 1.4 | **43.7** | 0 | 1.6 | 4.6 | 4.4 | 0.2 | 14.7 | 0.3 |
| *T. scabrum* | 0.969 | 1.7 | 0.1 | 0.1 | 0.2 | 0 | 0.5 | 0.1 | 6.4 | **15** | 0.3 | 9.5 | 2 | 0.2 | 7.1 | 0.5 |
| *T. scandens* | 0.959 | 0 | 0 | 0.3 | 9.2 | 8.1 | 1.7 | 0.6 | 0.1 | 7.8 | 0 | 0 | 15.2 | 0.9 | 7.6 | 14.4 |
| *T. schumannianum* | 0.998 | 2.9 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | **72.9** | 1.1 | 0 | 0 | 0 | 3.7 | **60.4** |
| *T. sedifolium* | 0.992 | 1.9 | 2 | 0 | 0 | 0 | 0 | 0.1 | 18.8 | 40.8 | 0.3 | 9.5 | 0.1 | 4.3 | **55.9** | 0 |
| *T. selagineum* | 0.955 | 0 | 0 | 1.3 | 0 | 0.8 | **16.3** | 0 | 0 | 0 | 0.6 | 0 | **77.1** | 0 | 9.8 | **13.2** |
| *T. sertulariastrum* | 0.911 | 2.9 | 3.7 | 0 | 13.4 | 0 | 0 | 0 | 7.5 | **58.5** | 0 | 0 | 0.3 | 0 | 2.6 | 19.4 |
| *T. spicatum* | 0.963 | 0 | 2.6 | 0 | 0.4 | 0.6 | 5.4 | 0.1 | 4.8 | **39.3** | 1.3 | 0.2 | 3.6 | 0.2 | 3.9 | 0 |
| *T. spinosum* | 0.92 | 4.4 | 7.2 | 0 | **17.8** | 0.2 | 0.9 | 0 | 1.6 | 17.2 | 2 | 0.1 | 0 | 0.1 | **13.7** | 0 |
| *T. spinulosum* | 0.95 | 0.4 | 1.2 | 0 | 0 | 2.1 | 5.8 | 0.1 | 20.4 | 6.9 | 1.1 | **29.4** | 0 | 0 | 0.9 | **40.5** |
| *T. squarrosum* | 0.973 | 0 | 0 | 0 | 0.4 | 0 | 0 | 0 | 0 | 1.1 | **23** | 0 | 0.7 | 16.9 | **43.2** | 5.3 |

| | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *T. stirtonii* | 0.985 | 0 | 0 | 0.5 | **23.3** | 0 | 0 | **60.2** | 0 | 10 | 0 | 0 | 5.9 | 0 | 8.8 | **23.8** |
| *T. strictum* | 0.901 | 1.4 | 2.6 | 1.3 | 1.2 | 1.8 | 2.3 | 1.7 | **23.1** | 18.6 | 2.5 | 7.5 | 1 | 1.5 | 15.3 | **42.7** |
| *T. subnudum* | 0.907 | 2 | 0.8 | 0.5 | 1.1 | 3 | 15.3 | 1.4 | 4 | **25.6** | 0.5 | 5.7 | 0 | 2.7 | 0.1 | 0 |
| *T. susannae* | 0.987 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | **64.7** | 0 | 5.2 | 0 | 0 | 0 | 6.3 | **27.5** |
| *T. translucens* | 0.975 | 8.4 | 1.4 | 0 | 0.9 | 0.1 | 0 | 0.1 | **45.3** | **23.7** | 0 | 5.1 | 0 | 8.3 | 2.3 | **35.3** |
| *T. triflorum* | 0.979 | 4.9 | 5.6 | 0 | **41.2** | 10.4 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | **30.1** | 0.1 |
| *T. umbelliferum* | 0.956 | **18.4** | 0 | 0 | 0 | 0 | 0 | 6.9 | 0 | 0 | 0 | **74.3** | 0 | 0 | 0.9 | 5.9 |
| *T. urceolatum* | 0.947 | **19.9** | 9.8 | 0 | 0 | 0 | 8.6 | 0 | 0.6 | 0.2 | 0 | 0 | 13.4 | 9.9 | **37.6** | 0.1 |
| *T. virgatum* | 0.909 | 1 | 0.4 | 0.9 | 0.5 | 0.4 | 3.7 | 1.7 | 17.3 | **36.6** | 2.6 | 5.6 | 0.7 | 0.8 | 0.3 | 0 |
| *T. viridifolium* | 0.998 | 0.3 | 1.7 | 0.9 | 0.9 | 0 | 0.1 | 0.1 | 2 | **73.8** | 1.2 | 0 | 0.2 | 0 | **37.6** | 0 |
| *T. whitehillensis* | 0.93 | 0 | 0 | 0 | 0 | **31.1** | 0 | 0 | 0 | 0 | **42.8** | 0 | 0 | 0 | 2.6 | **25.3** |
| **Average** | **0.925** | | | | | | | | | | | | | | | |




**Appendix Fig. S5.2:** The environmental variable response curves for the GCFR *Thesium* species. The response curves were based on the Maxent models. The x-axis are the variables that are discriminatory to distribution of the species whereas the y-axis shows the predictive value of the variable.

**Appendix Table S5.6:** Modelled predictions of range sizes during the Last Glacial Maxima (past), at present and future (to the year 2080) and the percentage differences. The extent of occurrence (EOO) obtained from GeoCat and the associated risk status of each species is also provided.

| species | past | present | future | future-present | % diff. | EOO | risk status | previous |
|---|---|---|---|---|---|---|---|---|
| *T. acuminatum* | 68 | 48 | 55 | 7 | 12.73 | 9920.74 | VU | LC |
| *T. aggregatum* | 656 | 534 | 662 | 128 | 19.34 | 153680 | LC | LC |
| *T. albomontanum* | 396 | 290 | 358 | 68 | 18.99 | 9250.87 | VU | LC |
| *T. annulatum* | 961 | 984 | 870 | -114 | -13.1 | 3193.53 | EN | DDT |
| *T. archeri* | 4583 | 2043 | 4467 | 2424 | 54.26 | 4444.21 | EN | LC |
| *T. bathyschistum* | 306 | 235 | 235 | 0 | 0 | 37215.3 | NT | DDT |
| *T. brachygyne* | 423 | 373 | 381 | 8 | 2.1 | 47445.6 | LC | DDT |
| *T. capitatum* | 430 | 386 | 411 | 25 | 6.08 | 116841 | LC | LC |
| *T. capitellatum* | 756 | 504 | 785 | 281 | 35.8 | 14783.8 | VU | LC |
| *T. capituliflorum* | 478 | 515 | 461 | -54 | -11.71 | 109660 | LC | LC |
| *T. carinatum* | 695 | 667 | 727 | 60 | 8.25 | 113150 | LC | NE |
| *T. commutatum* | 190 | 179 | 175 | -4 | -2.29 | 82951.1 | LC | LC |
| *T. densiflorum* | 249 | 234 | 206 | -28 | -13.59 | 86269.4 | LC | LC |
| *T. disciflorum* | 2316 | 3182 | 3542 | 360 | 10.16 | 71861.9 | LC | LC |
| *T. dissitiflorum* | 3038 | 1915 | 2025 | 110 | 5.43 | 12054.1 | VU | LC |
| *T. diversifolium* | 380 | 367 | 426 | 59 | 13.85 | 5989.43 | VU | DDT |
| *T. dmmagiae* | 17 | 14 | 14 | 0 | 0 | 7.325 | CR | NE |
| *T. ecklonianum* | 740 | 593 | 633 | 40 | 6.32 | 2152.56 | EN | EN |
| *T. elatius* | 769 | 787 | 724 | -63 | -8.7 | 53823.8 | LC | LC |
| *T. ericaefolium* | 645 | 560 | 651 | 91 | 13.98 | 189394 | LC | LC |
| *T. euphorbioides* | 373 | 343 | 293 | -50 | -17.06 | 48822.4 | LC | LC |
| *T. euphrasioides* | 151 | 131 | 111 | -20 | -18.02 | 13168.1 | VU | LC |
| *T. fallax* | 594 | 567 | 300 | -267 | -89 | 2704.24 | EN | DDD |
| *T. flexousum* | 1248 | 1084 | 1085 | 1 | 0.09 | 192290 | LC | LC |
| *T. foliosum* | 497 | 530 | 514 | -16 | -3.11 | 46278.9 | LC | LC |
| *T. fragile* | 641 | 526 | 557 | 31 | 5.57 | 118725 | LC | DDT |
| *T. frisea* | 741 | 609 | 689 | 80 | 11.61 | 76380.6 | LC | DDT |
| *T. frisea var. thunbergii* | 423 | 246 | 398 | 152 | 38.19 | 7305.1 | VU | LC |
| *T. fructicosum* | 524 | 1600 | 1308 | -292 | -22.32 | 31369.8 | NT | LC |
| *T, fruticulosum* | 782 | 680 | 743 | 63 | 8.48 | 224055 | LC | LC |
| *T. funale* | 361 | 306 | 378 | 72 | 19.05 | 61019.5 | LC | LC |
| *T. galioides* | 1075 | 1564 | 1282 | -282 | -22 | 62988.3 | LC | LC |
| *T. glomeratum* | 1799 | 1877 | 1598 | -279 | -17.46 | 8862.45 | VU | DDT |
| *T. glomeruliflorum* | 367 | 400 | 366 | -34 | -9.29 | 13712.4 | VU | LC |
| *T. gnidiaceum* | 662 | 991 | 817 | -174 | -21.3 | 219200 | LC | LC |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *T. gnidiaceum var. zeyheri* | 579 | 760 | 969 | 209 | 21.57 | 686.344 | EN | DDT |
| *T. hillianum* | 1181 | 1350 | 1349 | -1 | -0.07 | 548.174 | EN | DDT |
| *T. hirtum* | 284 | 142 | 207 | 65 | 31.4 | 35149.8 | NT | LC |
| *T. hispidulum* | 538 | 431 | 434 | 3 | 0.69 | 23790.2 | NT | LC |
| *T. hollandii* | 996 | 385 | 1268 | 883 | 69.64 | 2692.23 | EN | DDT |
| *T. imbricatum* | 2317 | 2075 | 2634 | 559 | 21.22 | 97347.4 | LC | LC |
| *T. impeditum* | 1441 | 1104 | 1382 | 278 | 20.12 | 678027 | LC | LC |
| *T. junceum* | 1136 | 1213 | 1192 | -21 | -1.76 | 179077 | LC | LC |
| *T. juncifolium* | 722 | 633 | 718 | 85 | 11.84 | 125122 | LC | LC |
| *T. karooicum* | 5095 | 4826 | 5355 | 529 | 9.88 | 16320.3 | VU | LC |
| *T. leptocaule* | 867 | 1080 | 993 | -87 | -8.76 | 60430.5 | LC | DDT |
| *T. leptostachyum* | 3626 | 1617 | 2749 | 1132 | 41.18 | 0 | CR | DDT |
| *T. lisae-mariae* | 2473 | 1296 | 2423 | 1127 | 46.51 | 26650.5 | NT | DDT |
| *T. litoreum* | 438 | 529 | 403 | -126 | -31.27 | 5036.92 | VU | CR |
| *T. longicaule* | 1008 | 1189 | 1044 | -145 | -13.89 | 20286.5 | NT | NE |
| *T. macrostachyum* | 738 | 715 | 742 | 27 | 3.64 | 21919 | NT | LC |
| *T. microcarpum* | 2386 | 1744 | 2077 | 333 | 16.03 | 127046 | LC | DDT |
| *T. microcephalum* | | - | - | - | - | 0 | CR | DDT |
| *T. micromeria* | 995 | 979 | 810 | -169 | -20.86 | 6939.08 | VU | LC |
| *T. micropogon* | 2044 | 2014 | 1920 | -94 | -4.9 | 49991.3 | LC | DDD |
| *T. minus* | 843 | 770 | 732 | -38 | -5.19 | 43410.6 | NT | DDT |
| *T. namaquense* | 2209 | 2097 | 2398 | 301 | 12.55 | 89014.8 | LC | LC |
| *T. nigromantanum* | 996 | 1169 | 1063 | -106 | -9.97 | 68864.8 | LC | LC |
| *T. nigroperianthum* | 58 | 56 | 55 | -1 | -1.82 | 4,321 | EN | NE |
| *T. nudicaule* | 1869 | 1732 | 1726 | -6 | -0.35 | 178300 | LC | LC |
| *T. occidentale* | 4576 | 5544 | 4415 | -1129 | -25.57 | 39830.7 | NT | LC |
| *T. paniculatum* | 73 | 83 | 75 | -8 | -10.67 | 4114.41 | EN | LC |
| *T. paronychioides* | 1876 | 1622 | 1724 | 102 | 5.92 | 23794.2 | NT | LC |
| *T. patulum* | 843 | 739 | 749 | 10 | 1.34 | 216040 | LC | LC |
| *T. penicillatum* | 352 | 288 | 276 | -12 | -4.35 | 31495.2 | NT | LC |
| *T. pinifolium* | 139 | 184 | 124 | -60 | -48.39 | 25137 | NT | LC |
| *T. polycephalum* | 2262 | 1862 | 2087 | 225 | 10.78 | 4940.55 | EN | LC |
| *T. prostratum* | 136 | 186 | 162 | -24 | -14.81 | 4887.97 | EN | LC |
| *T. pseudovirgatum* | 123 | 108 | 98 | -10 | -10.2 | 7186.74 | VU | LC |
| *T. pubescens* | 841 | 811 | 762 | -49 | -6.43 | 75828.2 | LC | LC |
| *T. pycnanthum* | 317 | 302 | 288 | -14 | -4.86 | 26088.1 | NT | LC |
| *T. quartzicolum* | 1554 | 852 | 1853 | 1001 | 54.02 | 4.97 | CR | NE |
| *T. quinqueflorum* | 360 | 263 | 237 | -26 | -10.97 | 10051.8 | VU | DDT |
| *T. rariflorum* | 1612 | 1182 | 1404 | 222 | 15.81 | 12611.6 | VU | DDT |
| *T. rhizomatum* | 292 | 384 | 140 | -244 | 174.29 | 791.363 | EN | NE |
| *T. rufescens* | 385 | 390 | 328 | -62 | -18.9 | 1886.33 | EN | DDT |
| *T. sawae* | 456 | 440 | 463 | 23 | 4.97 | 6225695 | LC | NE |
| *T. scabrum* | 310 | 269 | 251 | -18 | -7.17 | 94235 | LC | LC |
| *T. scandens* | 1064 | 1486 | 1329 | -157 | -11.81 | 28789.2 | NT | LC |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *T. schumannianum* | 55 | 35 | 62 | 27 | 43.55 | 2240.47 | EN | DDT |
| *T. scirpioides* | 11556 | 11391 | 11389 | -2 | -0.02 | 0 | EN | NE |
| *T. sedifolium* | 234 | 193 | 190 | -3 | -1.58 | 14105.7 | VU | NE |
| *T. selagineum* | 1448 | 2851 | 1486 | -1365 | -91.86 | 335.55 | EN | DDT |
| *T. sertulariastrum* | 2001 | 1815 | 1631 | -184 | -11.28 | 38973.5 | NT | DDT |
| *T. spicatum* | 279 | 254 | 251 | -3 | -1.2 | 72221.4 | LC | LC |
| *T. spinosum* | 1324 | 1159 | 1007 | -152 | -15.09 | 69214 | LC | LC |
| *T. spinulosum* | 351 | 321 | 294 | -27 | -9.18 | 83486 | LC | LC |
| *T. squarrosum* | 741 | 727 | 725 | -2 | -0.28 | 15814.4 | VU | LC |
| *T. stirtonii* | 463 | 594 | 383 | -211 | -55.09 | 3097.34 | EN | NE |
| *T. strictum* | 1556 | 1511 | 1596 | 85 | 5.33 | 322148 | LC | VU |
| *T. subnudum* | 1787 | 1798 | 1813 | 15 | 0.83 | 105763 | LC | LC |
| *T. susannae* | 146 | 157 | 167 | 10 | 5.99 | 1087.33 | EN | Rare |
| *T. translucens* | 494 | 451 | 447 | -4 | -0.89 | 34266.1 | NT | LC |
| *T. triflorum* | 708 | 636 | 743 | 107 | 14.4 | 10333.5 | VU | LC |
| *T. umbelliferum* | 1380 | 1336 | 1584 | 248 | 15.66 | 49661.6 | LC | LC |
| *T. urceolatum* | 2446 | 3252 | 2895 | -357 | -12.33 | 51190.8 | LC | DDT |
| *T. virgatum* | 1216 | 1232 | 1266 | 34 | 2.69 | 147949 | LC | LC |
| *T. viridifolium* | 72 | 58 | 58 | 0 | 0 | 1594.74 | EN | LC |
| *T. whitehillensis* | 5318 | 3954 | 2846 | -1108 | -38.93 | 5154.74 | VU | LC |

**Appendix 6a – Contribution to co-authored publications**

13 Nov 2019

To Whom It May Concern

We hereby confirm that the first author of the underlisted articles was principal in the work done toward publishing the articles:

i. **Zhigila, D.A.,** Verboom, G.A., Stirton, C.H. and Muasya, A.M. 2019. A taxonomic revision of *Thesium* section *Hagnothesium* (Santalaceae) and description of a new species, *T. quartzicolum*. South African Journal of Botany 124: 280–303

ii. **Zhigila, D.A.,** Verboom, G.A., Stirton, C.H., Smith, H. and Muasya, A.M. 2019. Seven new *Thesium* (Santalaceae) species endemic to the Greater Cape Floristic Region, South Africa. Phytotax*a* 423 (4): 215–237.

iii. **Zhigila, D.A.,** Verboom, G.A. and Muasya, A.M. (accepted). An infrageneric classification of *Thesium* (Santalaceae) based on molecular phylogenetic data – TAXON

Mr Zhigila conceptualised and designed the research and autonomously conducted the experiments and analysed the data. He wrote the manuscripts and address editorial comments. The co-authors contributed to the work through providing special expertise, funds, facilities, supervision, and comments and suggestions on the manuscripts.

Sincerely,

A/Prof. AM Muasya
PhD Supervisor

A/Prof GA Verboom
PhD Co-Supervisor